INHERITANCE OF COMPONENTS OF RESISTANCE TO LATE LEAFSPOT IN PEANUT

BY

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Dedicated to my family, especially my parents, "Bambo ndi Mai" J. Chiyembekeza, for the sacrifices that made this achievement possible.

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INHERITANCE OF COMPONENTS OF RESISTANCE TO LATE LEAFSPOT IN PEANUT

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Chairman: Dr. David A. Knauft
Major Department: Agronomy

Early and late leafspot diseases, caused by Cercospora arachidicola (CA) Hori and Cercosporidium personatum (CP) [(Berk. and Curt.) Deighton] cause significant yield losses in peanut (Arachis hypogaea L.). Peanut germplasm with varying levels of resistance to these diseases has been identified. The present research was undertaken to study inheritance of components of resistance of latent period (LP), lesion diameter (LD), and amount of sporulation (SP) to late leafspot. The research also examined stability of resistance in two locations, Florida and Malawi. Four peanut genotypes, with varying levels of resistance to late leafspot were utilized. Crosses were made among these genotypes in a 4 x 4 diallel, with reciprocals. Backcrosses were made between the F_1 and parental lines to produce BC_1 and BC_2 populations. Three tetrafoliolate leaves from five randomly selected plants

from each cross were inoculated with CP conidia and monitored for the three components. Genetic analyses were carried out to determine the mode of inheritance of the components. Performance of the F_1, F_2, and backcross progenies was comparable to the best parental lines for all the components. Additivity was the predominant genetic effect occurring in more than half of the crosses. Narrow-sense heritability estimates averaged 0.60 for LP, 0.52 for LD, and 0.41 for SP. Realized heritability estimates averaged 0.69 for LP, 0.63 for LD, and 0.52 for SP. General combining ability was significantly higher than specific combining ability and reciprocal effects for all the components. Some crosses exhibited reciprocal cross differences. All components significantly correlated with each other. Latent period was negatively correlated with LD ($r=-0.55$) and SP ($r=-0.63$); LD was positively correlated with SP ($r=0.44$). Measurements of the components in Florida and Malawi were positively correlated with each other. In these crosses LP, LD, and SP were quantitatively inherited and that additive gene effects were of major importance in controlling these components of resistance. Therefore, selection of resistant genotypes would be possible in early generations. The components were stable across environments, indicating that the pathogen population was similar. Consequently, utilization of the Florida germplasm would be beneficial for developing late leafspot resistant cultivars in Malawi.

CHAPTER 1
INTRODUCTION

Peanut (Arachis hypogaea L.) is one of the principal food crops of the world. The crop is native to South America, where the genus Arachis is distributed over a wide range of environments from south of the Amazon to 34° S latitude and from the eastern coast to the eastern slopes of the Andes (Gregory et al., 1980).

Arachis hypogaea, also known as groundnut, peanut, monkeynut, and goobernut, is presently cultivated in over 80 countries from 40° N to 40° S latitudes in tropical and temperate regions of the world. The natural occurrence of all the other species of the genus Arachis is confined to the five South American countries: Argentina, Bolivia, Brazil, Paraguay, and Uruguay (Krapovickas, 1973; Gregory et al.,1965). The currently accepted center of origin for the genus is in the Mato Grosso area of Brazil, located just north and east of Paraguay (Wynne and Halward, 1989).

Currently there are twenty-four countries that each produce more than 3,000 tons of peanut annually. China leads the world in total production followed by India and the United States of America (Commodity Year Book, 1988). In many countries of the world peanut is grown on small farms and marginal lands. Also, many parts of the world lack well

adapted high-yielding and disease-resistant cultivars.

In most countries, peanut is used for confectionary and oil extraction purposes. The kernels contain 40%-50% oil, though the range for U.S. cultivars is between 44.8% and 58.3% (Young and Hammons, 1978). Among the cultivated types, bunch cultivars frequently have higher oil content than runner types. Wild species have a broader range, 46.5% to 63% (Cherry, 1977).

Peanut, as a leguminous plant, enriches the soil with nitrogen and is, therefore, valuable in crop rotations and soil management practices. It is also an effective cover crop for lands exposed to soil erosion. The aerial parts of the plant are an important fodder for livestock in many developing countries, particularly during the dry season when animal feed is not readily available.

Peanut is susceptible to many diseases. However, early leafspot, caused by Cercospora arachidicola Hori (CA), and late leafspot, caused by Cercosporidium personatum [(Berk. and Curt.) Deighton] (CP) are the most serious diseases of peanut throughout the world (Jackson and Bell, 1969; Garren and Jackson, 1973; McDonald and Raheja, 1980). Both pathogens are commonly present wherever peanut are grown (Feakin, 1973), but the incidence and severity of each varies with the locality and season.

The two foliar diseases are economically important for several reasons. When the diseases attack the crop, the

infected leaflets or leaves may abscise as a response to infection by the fungi. Consequently, the photosynthetic effectiveness of the plant is reduced following loss of light-intercepting surfaces (Woodroof, 1933). Some lines however, do have tolerance to abscission. They can have a greater amount of infection before defoliation. Boote et al. (1980) reported an 80% loss of leaf area index (LAI) for 119 day old "Early Bunch" peanut canopies naturally infected by Cercospora leafspot. Not only was light interception reduced considerably, but photosynthetic effectiveness of the remaining tissue was also reduced. The result of reduced photosynthesis is lower yield. The increased leaf litter may also stimulate growth of facultative peanut pathogens such as Sclerotium rolfsii Sacc. by providing a food base (Cole and Grimmer, 1977).

Peanut yield losses due to leafspot diseases are generally substantial, but vary considerably among locations and seasons throughout the world. Worldwide, losses range from 10% to over 50% (McDonald and Fowler, 1977). Shokes et al. (1983) and Knauft et al. (1986) have reported yield losses of more than 80% when fungicides are not used to control the diseases. In Malawi, yield losses of 50% and 80% have been reported on studies conducted on research stations and farmers' fields, respectively, when fungicides are not used to control the diseases (Ministry of Agriculture, Annual Report, 1986).

Although effective fungicides are available, most notably chlorothalonil (Bravo), their use increases peanut production costs and may not be economically feasible under low input subsistence agricultural production systems. Also, in recent years, considerable pressure has been placed on world agriculture to reduce the quantity of pesticides used because of concerns over environmental contamination. Suitable, low-cost strategies for reducing pesticide usage should be found. One important strategy is the utilization of genetic resources to develop cultivars with high levels of tolerance to diseases.

Abdou et al. (1974) reported that a high level of resistance or immunity exists within the genus Arachis to both species of the fungi. One peanut accession, within the species A. chacoense, is highly resistant to early leafspot. Another accession of A. cardenasii is immune to late leafspot. Both of these species are diploid but are cross-compatible with the tetraploid cultivated peanut forming sterile triploids. Hexaploids from crosses of cultivated peanut with A. chacoense, A. cardenasii, and other diploid species have been exposed to C. personatum in field trials in India and C. arachidicola in Malawi. Lines from the hexaploids of A. hypogaea x A. cardenasii were found resistant to both pathogens (Moss, 1977, 1980). Stalker and Wynne (1979) also reported resistant selections to both pathogens in 40-chromosome derivatives from an A. hypogaea x A. cardenasii

hybrid population.

Resistance to both early and late leafspot has been described in the cultivated peanut (Gorbet et al., 1982; Kornegay et al., 1980; Melouk et al., 1984; Subrahmanyam et al., 1983). Although original sources of resistance were low yielding, hybridization and selection produced peanut genotypes with higher yield potentials than the existing commercial cultivars without fungicide application (Gorbet et al., 1982). A cultivar with partial resistance to late leafspot, Southern Runner, has been released from the Florida breeding program (Gorbet et al., 1986).

Since resistance mechanisms from various sources differ (Chiteka et al., 1988), combining resistance genes from these sources may result in higher levels of resistance. Because a number of these sources have high yield potential, it may be possible to select high-yielding, leafspot-resistant genotypes from crosses among these sources.

Knowledge of the inheritance of the components of resistance would be useful to better understand the genetic systems controlling that inheritance. Effective selection based on resistance components can best be achieved when the genetic basis of resistance is known.

The present research was initiated to study inheritance of components of resistance to late leafspot using peanut lines with yield potentials of more than five tons per hectare. The research also examined stability of resistance

to CP in two locations, Gainesville, Florida, USA, located 29° 41' N latitude and 82° 20' W longitude and Malawi, Africa, located between 9° 45' S and 17° 5' S latitude and 32° 45' E and 36° E longitude. The studies were conducted during the summers of 1989 and 1990 at the University of Florida Agronomy Farm, Gainesville, and at the Chitedze Research Station and the Chitala and the Kasinthula experimental stations, in Malawi, during the 1990/91 growing season. Objectives of this research were 1) to determine inheritance of three components of resistance: latent period (time in days from inoculation to first sporulating lesion), lesion diameter (measurement of lesions in mm), and amount of sporulation (using a 1-5 scale developed by Subrahmanyam et al., 1982), on six generations of peanut populations (P_1, P_2, F_1, F_2, BC_1, and BC_2) from a full diallel with four parents of varying degrees of resistance to late leafspot and 2) to investigate variability of host genetic response to infection by late leafspot at the two locations, Florida, USA, and Malawi, Africa.

CHAPTER 2
HERITABILITY AND GENETIC EFFECTS OF COMPONENTS OF RESISTANCE TO LATE LEAFSPOT

Introduction

Late leafspot caused by the fungus Cercosporidium personatum [(Berk. and Curt.) Deighton] is one of the most destructive diseases of peanut in the southern United States. In Florida, late leafspot is the most economically significant disease, because of both loss in yield and the cost needed for control.

Hemingway (1955) reported that late leafspot was the more devastating pathogen in Tanzania even when both early and late leafspot occurred together. In Malawi, late leafspot is predominant in the low altitude areas of the country (50-750 m) and usually appears 40-50 d after seedling emergence (Ngwira, 1985).

Complete resistance to late leafspot has not been found in the cultivated species of Arachis, however rate-reducing resistance is available (Abdou et al., 1974; Anderson et al., 1986; Chiteka, 1987; Foster et al., 1980; Gorbet et al., 1990; Kornegay et al., 1980). Southern Runner, a peanut cultivar with resistance to late leafspot, has been released by the University of Florida (Gorbet et al., 1986), and also, advanced breeding lines with partial resistance to late

leafspot have been developed (Gorbet et al., 1982, 1990). Peanut yields near 5 tons ha^{-1} have been reported from these sources (Gorbet et al., 1982, 1990) compared to yields of less than 2 tons ha^{-1} from the leading commercial cultivar, Florunner, without fungicide application.

Higgins (1935) noted that selections with resistance to early leafspot were often susceptible to late leafspot. He concluded that resistance to the two pathogens was independently inherited. Monasterios (1980) found evidence that resistance to early leafspot was associated with susceptibility to late leafspot and vice versa, supporting the 1935 findings by Higgins. On the contrary, Anderson et al. (1986) found positive correlations among components of resistance to early and late leafspot and concluded that inheritance to the two pathogens is not independent.

Several components of resistance to late leafspot have been identified (Nevill, 1981; Subrahmanyam et al., 1985; Watson, 1987; Chiteka et al., 1988). Sharief et al. (1978) proposed a multifactorial genetic system controlling resistance to late leafspot in wild Arachis species. They stated that introgression of resistance factors from wild to cultivated species should yield useful genetic resistance. Nevill (1982) proposed a genetic model with five loci for resistance to late leafspot.

Additive gene action has been reported to be significant for late leafspot resistance (Jogloy et al., 1987; Walls et

al., 1985). Dominance was significant for the resistance components of lesion size, latent period, and sporulation from a generation means analysis on late leafspot (Jogloy, 1988).

Heritability estimates reported in the literature for components of resistance to late leafspot have been variable. Estimates of narrow-sense heritabilities have ranged from low to high (Iroume and Knauft, 1987; Jogloy, 1988; Jogloy et al., 1987) due to genotype by environment interactions especially when the tests were conducted in a single environment. Jogloy (1988) found that heritability estimates were variable among crosses tested and among components of resistance within crosses. Broad-sense heritability estimates for components of resistance reported by Anderson et al. (1986, 1991) ranged from low to high (0.40-0.80; 0.12-0.88); those reported by Jogloy et al. (1987) were low to moderate (0.13-0.68).

Prior to the present study, components of partial resistance to late leafspot (incubation period, latent period, lesion diameter, and amount of sporulation) for over a hundred peanut genotypes, including commercial cultivars, germplasm, and advanced breeding lines, were quantified under both field and greenhouse environments in Florida (Chiteka, 1987). Chiteka (1987) reported significant variability for each component in one or more of the studies conducted and concluded that latent period, amount of sporulation, and lesion diameter were the most consistent components to rate genotypes for resistance in different environments.

Selection for resistance on the basis of these components can be achieved most efficiently when the genetics of the components are understood. The objectives of this study were 1) to investigate the type of gene action that controls the three components of resistance to late leafspot, latent period, lesion diameter, and amount of sporulation, from six populations of peanut (P_1, P_2, F_1, F_2, BC_1, and BC_2) using generation means analysis and 2) to determine narrow-sense and realized heritability estimates by parent-offspring regression for these components in crosses among four peanut genotypes.

Materials and Methods

Peanut Genotypes

Four peanut genotypes were utilized in this study. The genotypes and criteria for inclusion in this study are given in Table 2-1. Data on disease reactions based on previous analysis of resistance components (Chiteka, 1987) are presented in Table 2-2. These genotypes were selected based on yield potential and range of rating for resistance components in different environments. Latent period, lesion diameter, and amount of sporulation were chosen as components to be studied based on the conclusions of Chiteka et al. (1988). They found these components to be reliable in rating genotypes for resistance to late leafspot.

Generation of Segregating Populations

Twelve crosses were made in the Fall of 1988 and 1989 utilizing the four genotypes (Table 2-1) in a 4 x 4 diallel,

Table 2-1. Peanut genotypes used to study inheritance of components of resistance to late leafspot in peanut and criteria for selection.

Identity	Genotype/Pedigree	Selection criteria
UF-P1	72 x 32B-3-2-1-2-b3-B (PI 259785 x Florigiant)	Long latent period, reduced lesion diameter, and reduced sporulation.
UF-P2	73 x 18A-5-2-3-2-1-1-2-b2-B (PI 268894 x 501A)	Intermediate between UF 81206-2 and Sunrunner (line 519-9).
UF-P3	UF 81206-2	Long latent period, reduced lesion diameter, and reduced sporulation
UF-P4	Sunrunner (line 519-9)	Commercially acceptable cultivar, high yielding with good market quality, but susceptible to CP.

Table 2-2. Comparison of four selected peanut genotypes based on three components of resistance: latent period, lesion diameter, and amount of sporulation.

Genotype	Latent period[1] (LS1) (a)	(LS2) (b)	Lesion diameter[2] (a)	(b)	Sporulation score[3] (a)	(b)
UF-P1	21.5	25.8	2.5	1.6	2.5	3.1
UF-P2	21.5	25.8	2.5	2.8	2.7	3.1
UF-P3	32.7	38.0	1.0	1.2	1.8	2.3
UF-P4	16.2	17.8	3.7	4.5	2.9	3.9

1 Measurement in days from inoculation to first (LS1) or second (LS2) sporulating lesion.
2 Measurement of lesions in mm, in the greenhouse at the North Florida Research Education Center (NFREC), Quincy (a) or in the field at Dozier Boy's School, Marianna (b).
3 Rating of sporulation based on a 1-5 scale in the greenhouse at the NFREC, Quincy (a) or in the field at the Dozier Boy's School, Marianna (b).
Source: Chiteka, 1987.

with reciprocals. The genotype and pedigree of the crosses are listed in Table 2-3. F_1 seed from the twelve crosses were harvested and dried in February, 1989. Ten seed from each cross were planted on 4 April 1989 at the University of Florida Agronomy Farm near Gainesville. Remaining F_1 seed were kept for backcrossing to the parental lines during the Fall of 1989. The backcross generations (BC_1 and BC_2) were required for the generation means analysis procedure. The backcross combinations generated are given in Table 2-4.

Assessment of Resistance

One greenhouse and four field studies were conducted between the summer of 1989 and the spring of 1991 at three locations. Two field studies were conducted in Gainesville, Florida, one in the summer of 1989 and the other during the summer of 1990. Two other field studies and one greenhouse study were carried out in Malawi, during the 1990/91 growing season. The field studies were conducted at Chitala and Kasinthula experimental stations while the greenhouse study was conducted at Chitedze Research Station (Figure 2-1). Chitala and Kasinthula were selected as experimental sites because of the high incidence of late leafspot in these areas. Also the climatic conditions of those areas are similar to those of Gainesville.

University of Florida

Field experiments were conducted at Green Acres, a University of Florida farm, approximately 20 km northwest of

Table 2-3. Description of crosses made among four peanut genotypes to study inheritance of components of resistance to late leafspot in peanut.

Cross No.	Genotype	Pedigree
1	C8801	UF-P1 x UF-P2
2	C8802	UF-P1 x UF-P3
3	C8803	UF-P1 x UF-P4
4	C8804	UF-P2 x UF-P3
5	C8805	UF-P2 x UF-P4
6	C8806	UF-P3 x UF-P4
7	C8807	UF-P2 x UF-P1
8	C8808	UF-P3 x UF-P1
9	C8809	UF-P3 x UF-P2
10	C8810	UF-P4 x UF-P1
11	C8811	UF-P4 x UF-P2
12	C8812	UF-P4 x UF-P3

Table 2-4. Description of backcross progeny combinations generated from 12 F_1 crosses used to study inheritance of components of resistance to late leafspot.

Cross No.	Genotype	Generation	Pedigree
1	C8901	BC_1	UF-P1 x (UF-P1 x UF-P2)
2	C8902	BC_2	UF-P2 x (UF-P1 x UF-P2)
3	C8903	BC_1	UF-P1 x (UF-P1 x UF-P3)
4	C8904	BC_2	UF-P3 x (UF-P1 x UF-P3)
5	C8905	BC_1	UF-P1 x (UF-P1 x UF-P4)
6	C8906	BC_2	UF-P4 x (UF-P1 x UF-P4)
7	C8907	BC_1	UF-P2 x (UF-P2 x UF-P3)
8	C8908	BC_2	UF-P3 x (UF-P2 x UF-P3)
9	C8909	BC_1	UF-P2 x (UF-P2 x UF-P4)
10	C8910	BC_2	UF-P4 x (UF-P2 x UF-P4)
11	C8911	BC_1	UF-P3 x (UF-P3 x UF-P4)
12	C8912	BC_2	UF-P4 x (UF-P3 x UF-P4)
13	C8913	BC_1	UF-P2 x (UF-P2 x UF-P1)
14	C8914	BC_2	UF-P1 x (UF-P2 x UF-P1)
15	C8915	BC_1	UF-P3 x (UF-P3 x UF-P1)
16	C8916	BC_2	UF-P1 x (UF-P3 x UF-P1)
17	C8917	BC_1	UF-P3 x (UF-P3 x UF-P2)
18	C8918	BC_2	UF-P2 x (UF-P3 x UF-P2)
19	C8919	BC_1	UF-P4 x (UF-P4 x UF-P1)
20	C8920	BC_2	UF-P1 x (UF-P4 x UF-P1)
21	C8921	BC_1	UF-P4 x (UF-P4 x UF-P2)
22	C8922	BC_2	UF-P2 x (UF-P4 x UF-P2)
23	C8923	BC_1	UF-P4 x (UF-P4 x UF-P3)
24	C8924	BC_2	UF-P3 x (UF-P4 x UF-P3)

Gainesville, Florida in 1989 and 1990. In 1989, F_1 seed together with the four parental lines were planted in one replicate and in single row plots. The F_1 seed were treated with ethrel and pre-germinated in the greenhouse prior to planting. The seedlings were transplanted on 14 April 1989. The seedlings were planted 30 cm apart in rows 6.1 m long, spaced 0.91 m apart. Southern Runner (a genotype with partial resistance to late leafspot) was planted around the experiment. The genotypes were evaluated for the three components of resistance.

In the summer of 1990, F_1 seed from 1989 crosses, F_2 seed from the 1989 field evaluation, and seed from backcrosses (BC_1 and BC_2) together with the parental lines were also evaluated at the University of Florida Agronomy Farm. In 1990, single row plots were utilized. The genotypes were planted on 4 April 1990 at a rate of 20 seed per 6.1 m row, spaced 0.91 m apart. A randomized complete block design with two replications was utilized.

Weekly rainfall accumulated at Gainesville during the summers of 1989 and 1990 is shown in Figure 2-2. However, supplemental irrigation was applied whenever necessary. Standard cultural practices for peanut production in Florida (Whitty et al., 1975) were followed with the exception that fungicides were not applied.

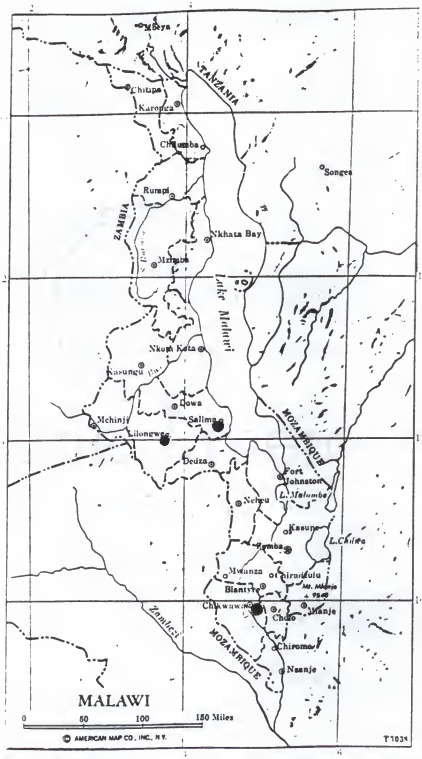

Figure 2-1 Map of Malawi. Large dots indicate the locations of research stations where studies on inheritance of components of resistance to late leafspot in peanut were conducted during the 1990/91 growing season.
Source: American Map Co. Inc. NY, USA.

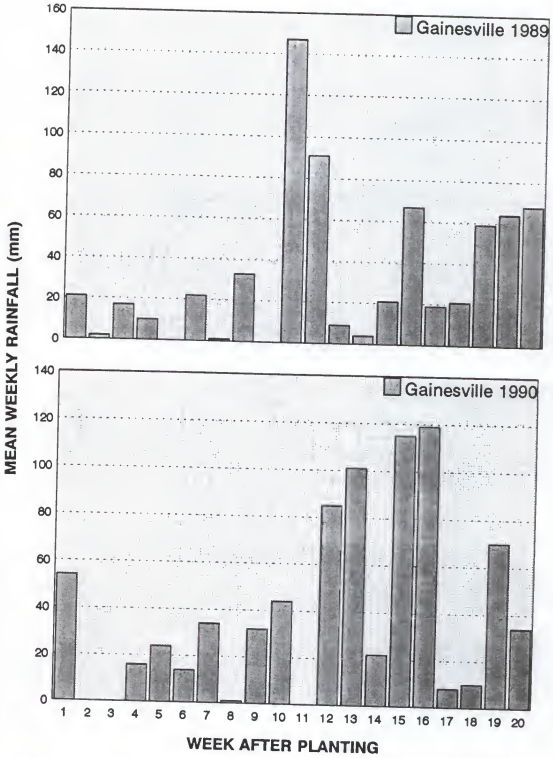

Figure 2-2 Mean weekly rainfall accumulated (mm) at Green Acres farm, Gainesville, Florida, during the summers of 1989 and 1990.

Greenhouse and Field Studies in Malawi

F_2 and F_3 seed from the summer 1990 UF study, together with the four parental lines, were evaluated in Malawi both in greenhouse and field during the 1990/91 growing season. The greenhouse study was conducted at Chitedze Research Station, located 16 km west of Lilongwe (Figure 2-1). The genotypes (F_2, F_3, and parental lines) were planted in 15 cm pots on 15 October 1990. Pots were arranged on a greenhouse bench in a randomized complete block design with three replications. The plants were watered as necessary throughout the experimental period. One of the field studies was conducted at Chitala experimental station in Salima district, located 112 km northeast of Lilongwe; the other study was conducted at Kasinthula experimental station in Chikwawa district, located 405 km south of Lilongwe (Figure 2-1). In both field studies a randomized complete block design with three replications was utilized. Each plot consisted of two 6.0 m long ridges, spaced 0.91 m apart. Seed were planted at the rate of 20 seed per 6.0 m ridge. The experiment at Kasinthula was planted on 20 November 1990 and that at Chitala was planted on 27 December 1990. The planting was staggered to allow ample time for data collection at each site. The field at Kasinthula received supplemental irrigation whenever necessary while the field at Chitala was exclusively rainfed. Figure 2-3 shows the weekly amount of rainfall accumulated during the 1990/91 growing season at Kasinthula and Chitala. Standard cultural

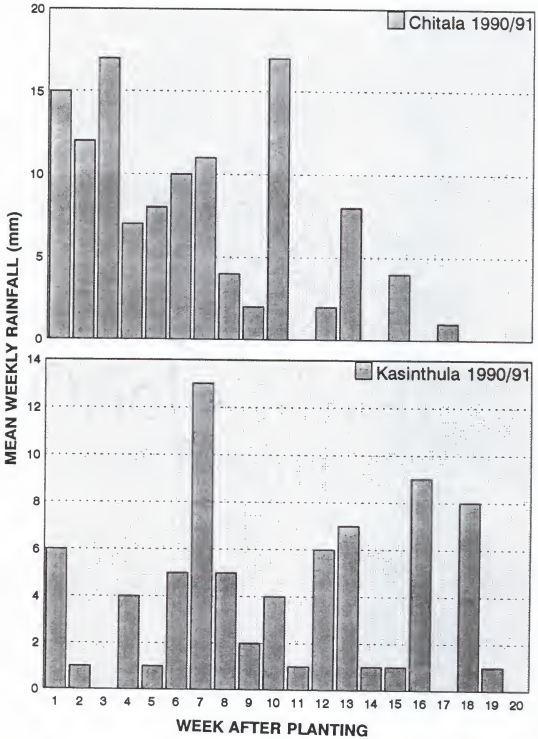

Figure 2-3 Mean weekly rainfall accumulated (mm) at Chitala and Kasinthula experimental stations, Malawi, during the 1990/91 growing season.

practices for peanut production in Malawi (Chiyembekeza and Sibale, 1986) were followed. However, fungicides were not applied at either experimental site.

Inoculum Production and Inoculation

Inoculum for the UF study was provided by Dr. F.M. Shokes of the North Florida Research and Education Center, Quincy. The inoculum was produced on a susceptible cultivar, Early Bunch, following the procedure outlined by Chiteka et al. (1988). For the study in Malawi, inoculum was produced on Malimba, a susceptible cultivar, raised by Dr. P. Subrahmanyam of the Southern Africa Development Coordinating Conference--International Crops Research Institute for the Semi-Arid Tropics (SADCC/ICRISAT) Regional Groundnut Program for Southern Africa, Lilongwe, Malawi. In each study, one month after planting, five plants from each plot were randomly selected and marked with flags.

From each selected plant, three fully expanded tetrafoliolate leaves were tagged. Inoculum was obtained from the source plants raised in the greenhouse for both the UF field studies and the Malawi field and greenhouse studies. Conidia were collected from sporulating lesions using a cyclone spore collector. Conidia were suspended in distilled water and diluted to 5,000 spores mL^{-1}. A drop of Tween 80 per 100 mL of mixture was added to the conidial suspension to ensure an even spread of inoculum on the leaf surfaces.

Inoculation was made with a Spra Tool (Fisher Scientific Products, Pittsburgh, PA) calibrated to deliver 1 mL of inoculum per tetrafoliolate leaf.

The target leaf was held flat on a wooden board and the adaxial surface was sprayed with the spore suspension for one second. Inoculations for each experiment were completed on the same day. In the UF studies, inoculations were made on 15 May 1989 and 5 May 1990. In Malawi, the greenhouse study at Chitedze was inoculated on 16 November 1991; for the field studies, inoculations were made on 23 December 1990 and 30 January 1991, for Kasinthula and Chitala, respectively. Inoculated leaves were used to monitor the components of resistance for 35 to 40 d after each inoculation. Each target leaf was examined every two to three days beginning five days following inoculation.

Data were collected on the following three components of resistance:

1) latent period (LP)--measured as number of days from inoculation to the first sporulating lesion,

2) lesion diameter (LD)--mean diameter (mm) of two lesions randomly selected from each tetrafoliolate leaf,

3) amount of sporulation (SP)--mean amount of sporulation on two lesions measured after 72 h of incubation, based on a 1-5 scale according to Subrahmanyam et al. (1982), where,

1 = few stromata with little or no sporulation

2 = few stromata with slight sporulation

3 = stromata over most of lesion, moderate sporulation

4 = stromata on entire lesion, moderate to profuse sporulation

5 = dense production of stromata with heavy sporulation.

Sporulating lesions were identified on the target leaves with a (20x) magnifying lens. Latent period was recorded on those genotypes. The leaves were excised from the plant and lesion diameter was measured on two randomly selected lesions from each tetrafoliolate leaf using a transparent ruler. The measured lesions were marked with a felt tip marker; the leaves were then placed in a moist chamber (Ziploc bag with moist filter paper). All sample bags were placed in a large plastic bag and incubated at room temperature for 72 h. Thereafter, the two marked lesions on each leaf were scored for sporulation using a (10x) dissecting microscope.

Statistical Analyses

Data collected for each of the three components from the parental lines, F_1, F_2, F_3, and backcross populations [BC_1 (P_1F_1) and BC_2 (P_2F_1)] for each replicate were used as data entries for statistical analyses.

Generation Means Analysis

Generation means analysis (Jennings et al., 1974) was done to estimate the magnitude of gene effects. A weighted least squares program (Rowe and Alexander, 1980) for estimating genetic parameters was utilized. A six parameter

model (Gamble, 1962) comprising means of six populations, P_1, P_2, F_1, F_2, BC_1, and BC_2 was fitted to the data. The six generations were used to obtain estimates of six genetic parameters:

$$m = F_2$$

$$a = P_1F_1 - P_2F_1$$

$$d = -1/2P_1 + 1/2P_2 + F_1 - 4F_2 + 2P_1F_1 + 2P_2F_1$$

$$aa = -4F_2 + 2P_1F_1 - 2P_2F_1$$

$$ad = -1/2P_1 + 1/2P_2 + P_1F_1 - P_2F_1$$

$$dd = P_1 + P_2 + 2F_1 + 4F_2 - 4P_1F_1 - 4P_2F_1$$

The six genetic parameters are defined as follows: m = the midparent value or F_2 mean, a = the amount of variation among the means resulting from the additive effects of the genes, d = the amount of variation among the means resulting from the dominance effects of the genes, aa = the amount of variation among the means due to the additive x additive epistatic effects, ad = the amount of variation among the means resulting from additive x dominance epistatic effects, and dd = the amount of variation among the means resulting from dominance x dominance epistatic effects. The expected coefficients of the gene effects from this analysis are given in Table 2-5.

Estimates of the generation means used in the analysis were obtained after averaging the replicates. The generation means were weighted (Mather and Jinks, 1983) to account for any unequal variances among generations and to obtain the best

Table 2-5. Coefficients of gene effects in an analysis of generation means with six generations.

	Gene effects					
Generation	m	a	d	aa	ad	dd
P_1	1	1	0	1	0	0
P_2	1	-1	0	1	0	0
F_1	1	0	1	0	0	1
F_2	1	0	0.50	0	0	0.25
BC_1	1	0.50	0.25	0.25	0.25	0.25
BC_2	1	-0.50	0.50	0.25	-0.25	0.25

estimates of gene effects. Significance of the genetic estimates was determined by comparing the estimated values with their standard errors. If the absolute value of an estimate exceeded twice its standard error, the estimate was considered significantly different from zero (Gellner and Sechler, 1986).

Regression Analyses

To determine narrow-sense heritability for the three components of resistance studied, the parent-offspring regression analysis (Smith and Kinman, 1965) was used. F_1 and F_2 data from the Gainesville 1990 study, and F_2 and F_3 data from the Malawi 1990/91 studies were used for the analyses. The correct estimator equation is given as $h^2 = b/2r_{xy}$, where r_{xy} is a measure of the degree of genetic relationship between the parent, Y and its offspring, X.

To determine the magnitude of the narrow-sense heritability estimates, realized heritability estimates (Jennings et al., 1974) were calculated. These were estimated as:

$H_R = D_2/D_1 = X's - X_2/Xs - X_1$, where D_1 = selection differential between a selected sample mean (Xs) and the overall mean X_1 of the F_2 and D_2 = differential (observed gain) between the mean of the selfed progenies of Xs (X's) and the overall mean (X_2) of the F_3. The selection intensity was 10%.

Results and Discussion

Generation Means

The mean LP, LD, and SP measurements of the six generations are presented in Tables 2-6, 2-7, and 2-8, respectively. In the cross designation, the first parental line was considered as P_1, and the second parent as P_2.

In general, the performance of the F_1, F_2, and the backcross generations was comparable to the best parental line for all the components. Cross UF-P2 x UF-P1 performed significantly better than both parental lines in the F_1, F_2, and BC_1 generations for LP while cross UF-P3 x UF-P2 performed better for LP in the F_1, F_2, and BC_2 generations; the same crosses also performed better for LD. However, cross UF-P3 x UF-P2 performed better than or equal to the parental lines for SP in the F_1, BC_1, and BC_2 generations (Tables 2-6, 2-7, and 2-8).

An analysis of variance was done on the six generations, P_1, P_2, F_1, F_2, BC_1, and BC_2 to test the significance of the differences among the generation means for each component. The replication x generation interaction was used as an estimate of experimental error for the replication and generations. The pooled error was used to test the significance of the replication x generation interaction. Mean squares from the analysis are presented in Table 2-9.

Since genetic variation existed among the generations (Table 2-9), further analysis (Gamble, 1962) was done to

Table 2-6. Mean latent period (LP) measured on six generations, P_1, P_2, F_1, F_2, BC_1, and BC_2 in the field study on inheritance of components of resistance to late leafspot conducted at Gainesville, Florida, 1990.

Crosses	Generations					
	P_1	P_2	F_1	F_2	BC_1	BC_2
	days					
UF-P1 x UF-P2	30.4	27.5	26.9	29.0	26.4	27.0
UF-P1 x UF-P3	30.4	32.8	27.0	29.0	24.1	25.0
UF-P1 x UF-P4	30.4	25.7	27.1	25.3	28.8	26.9
UF-P2 x UF-P3	27.5	32.8	30.7	31.9	28.9	29.0
UF-P2 x UF-P4	27.5	25.7	24.9	24.7	25.8	29.9
UF-P3 x UF-P4	32.8	25.7	26.5	21.7	25.8	27.6
UF-P2 x UF-P1	27.5	30.4	31.6	32.3	33.0	29.6
UF-P3 x UF-P1	32.8	30.4	27.7	28.8	29.9	29.2
UF-P3 x UF-P2	32.8	27.5	33.3	28.1	31.4	35.5
UF-P4 x UF-P1	25.7	30.4	27.5	29.4	26.5	26.6
UF-P4 x UF-P2	25.7	27.5	29.6	27.0	30.5	30.0
UF-P4 x UF-P3	25.7	32.8	32.2	29.9	29.8	27.3
Means	-	-	28.8	28.1	28.4	28.6
LSD (0.05)	-	-	2.7	2.9	2.8	2.6

Table 2-7. Mean lesion diameter(LD) measured on six generations, P_1, P_2, F_1, F_2, BC_1, and BC_2 in the field study on inheritance of components of resistance to late leafspot conducted at Gainesville, Florida, 1990.

Crosses	Generations					
	P_1	P_2	F_1	F_2	BC_1	BC_2
	mm					
UF-P1 x UF-P2	2.3	2.3	2.6	2.3	2.5	2.1
UF-P1 x UF-P3	2.3	1.8	1.9	1.3	2.3	2.3
UF-P1 x UF-P4	2.3	2.4	2.2	2.2	2.0	2.2
UF-P2 x UF-P3	2.3	1.8	2.0	1.8	2.2	1.9
UF-P2 x UF-P4	2.3	2.4	2.4	2.3	2.4	2.4
UF-P3 x UF-P4	1.8	2.4	1.9	2.3	2.3	2.1
UF-P2 x UF-P1	2.3	2.3	2.0	1.8	2.0	2.1
UF-P3 x UF-P1	1.8	2.3	2.1	2.1	1.9	2.0
UF-P3 x UF-P2	1.8	2.3	1.7	2.1	1.8	1.8
UF-P4 x UF-P1	2.4	2.3	2.4	2.4	2.3	2.2
UF-P4 x UF-P2	2.4	2.3	2.0	2.3	2.1	2.2
UF-P4 x UF-P3	2.4	1.8	1.9	1.7	2.0	2.1
Means	-	-	2.1	2.1	2.2	2.1
LSD (0.05)	-	-	0.3	0.3	0.3	0.3

Table 2-8. Mean sporulation score (SP) measured on six generations, P_1, P_2, F_1, F_2, BC_1, and BC_2 in the field study on inheritance of components of resistance to late leafspot conducted at Gainesville, Florida, 1990.

Crosses	Generations					
	P_1	P_2	F_1	F_2	BC_1	BC_2
	1-5 scale					
UF-P1 x UF-P2	2.4	2.2	2.6	2.3	2.6	2.5
UF-P1 x UF-P3	2.4	1.8	2.0	2.0	2.6	2.6
UF-P1 x UF-P4	2.4	2.6	2.5	2.4	2.4	3.2
UF-P2 x UF-P3	2.2	1.8	2.1	2.2	2.4	2.2
UF-P2 x UF-P4	2.2	2.6	2.7	2.7	2.6	2.5
UF-P3 x UF-P4	1.8	2.6	2.3	2.2	2.2	2.7
UF-P2 x UF-P1	2.2	2.4	2.3	2.0	2.7	2.5
UF-P3 x UF-P1	1.8	2.4	2.4	2.2	2.2	2.3
UF-P3 x UF-P2	1.8	2.2	1.7	2.5	1.8	1.6
UF-P4 x UF-P1	2.6	2.4	2.4	2.6	2.8	2.4
UF-P4 x UF-P2	2.6	2.2	2.5	2.6	2.4	2.4
UF-P4 x UF-P3	2.6	1.8	2.2	2.1	2.8	2.6
Means	-	-	2.3	2.3	2.5	2.5
LSD (0.05)	-	-	0.4	0.4	0.4	0.4

Table 2-9. Mean squares from generation means analysis for three components of resistance, latent period (LP), lesion diameter (LD), and amount of sporulation (SP) to late leafspot.

Source of variation	df	Component[a]	Mean squares
Replication	1	LP	666.92*
		LD	2.37*
		SP	0.58
Generation	5	LP	199.75***
		LD	1.18**
		SP	2.52**
Rep. x Gen.	5	LP	189.21***
		LD	1.08**
		SP	2.24***
Pooled error	58	LP	34.24
		LD	0.34
		SP	0.52

*, **, *** Denote significance at the 0.05, 0.01, and 0.001 probability levels, respectively.
[a] LP = measurement in days, LD = measurement in mm, and SP = leafspot rating on a 1-5 scale.

estimate gene effects. The generation means approach primarily relates to the mode of gene action in the quantitative traits, particularly with the combinations of epistatic effects to heterosis in single cross hybrids. Gene effects computed for each component of resistance are presented in Tables 2-10, 2-11, and 2-12. Instead of attaching standard errors of the estimates, the significant estimates have been indicated in their usual manner.

It should be noted that the negative sign appearing on the gene effects depends upon the parents being considered as P_1 or P_2. If the value of P_1 is larger than P_2, the estimate will be positive and if the value of P_1 is smaller than P_2 then the value will be negative. The mean (m) is a statistical midparent, defined as the F_2 generation mean. Estimates of these genetic effects were derived from the means of the generations evaluated by solving equations given earlier for each effect using the coefficients presented in Table 2-5. The significance of each effect was tested by a two-tailed t-test.

The statistical midpoint, defined earlier as the mean of the F_2 generation was significant in all cases. This implies that the mean F_1 rating for all the components was different from zero. The analysis indicated that additivity was the predominant genetic effect occurring in more than half of the crosses. Nine of the twelve crosses exhibited additivity for LP and LD; eight crosses showed additivity for SP. The other

Table 2-10. Mean estimates of six gene effects for measurements on latent period (LP) for twelve crosses, in the field study conducted at Gainesville, Florida, 1990.

Crosses	Gene effects					
	m	a	d	aa	ad	dd
	days					
UF-P1 x UF-P2	29.0**	-0.6**	-12.0*	-9.4	-2.2	3.4
UF-P1 x UF-P3	27.0**	-0.8**	-9.5	-9.8	1.0	31.7**
UF-P1 x UF-P4	25.3**	1.9**	7.9	10.4*	1.5	-16.7
UF-P2 x UF-P3	27.9**	-0.1	5.8	4.1	3.3	-3.2
UF-P2 x UF-P4	24.7**	-4.1**	10.7	12.5*	-3.1	-23.4**
UF-P3 x UF-P4	31.7**	-1.8**	-20.1**	-20.1**	-4.2	30.7**
UF-P2 x UF-P1	32.3**	3.4**	-2.1	-4.2	4.9	-10.7
UF-P3 x UF-P1	28.8**	0.7*	-0.9	3.0	-1.1	-9.5
UF-P3 x UF-P2	28.1**	-4.0**	26.2**	21.3**	-7.4*	-31.8**
UF-P4 x UF-P1	29.4**	-0.1	-13.1*	-11.2*	0.4	11.5
UF-P4 x UF-P2	27.0**	0.5	14.8*	13.2*	-0.5	-27.2**
UF-P4 x UF-P3	25.9**	2.5*	11.6*	10.7*	4.8	-5.6

*, ** Denote significance at the 0.05 and 0.01 probability levels, respectively.

Table 2-11. Mean estimates of six gene effects for measurements on lesion diameter (LD) for twelve crosses, in the field study conducted at Gainesville, Florida, 1990.

Crosses	Gene effects					
	m	a	d	aa	ad	dd
	mm					
UF-P1 x UF-P2	2.3**	0.4**	0.6*	0.2	0.4*	0.3
UF-P1 x UF-P3	2.3**	0.1*	0.1	0.2	-0.1	-1.6**
UF-P1 x UF-P4	2.2**	-0.2**	-0.1	-0.2	-0.1	1.0
UF-P2 x UF-P3	2.0**	0.0	0.1	0.2	0.1	-0.6
UF-P2 x UF-P4	2.3**	0.3**	0.2	0.2	0.1	-0.8
UF-P3 x UF-P4	2.3**	0.2**	-0.4	-0.3	0.4*	-0.7
UF-P2 x UF-P1	1.8**	-1.5*	0.9*	1.0	-0.2	-0.5
UF-P3 x UF-P1	2.1**	-0.1*	-0.5*	-0.7	0.1	1.0
UF-P3 x UF-P2	2.1**	0.0	-1.5**	-1.3	0.3	1.8**
UF-P4 x UF-P1	2.4**	0.1	-0.3	-0.5*	0.1	0.7*
UF-P4 x UF-P2	2.3**	-0.2**	-0.5*	-0.5*	-0.1	0.9*
UF-P4 x UF-P3	2.2**	0.1*	-0.9*	-0.7*	-0.3	0.3

*, ** Denote significance at the 0.05 and 0.01 probability levels, respectively.

Table 2-12. Mean estimates of six gene effects for measurements on sporulation score (SP) for twelve crosses, in the field study conducted at Gainesville, Florida, 1990.

Crosses	Gene effects					
	m	a	d	aa	ad	dd
	1-5 scale					
UF-P1 x UF-P2	2.3**	0.1*	1.2*	0.9*	0.1	-1.3
UF-P1 x UF-P3	2.4**	0.0	0.8	0.8	-0.3	-3.1**
UF-P1 x UF-P4	2.4**	-0.8**	1.8**	1.4*	-0.8*	-2.5**
UF-P2 x UF-P3	2.2**	0.2*	0.1	0.3	-0.2	-0.9
UF-P2 x UF-P4	2.7**	0.1	-0.5	-0.8	0.1	0.4
UF-P3 x UF-P4	2.2**	-0.5**	1.0*	0.9*	-0.2	-2.5**
UF-P2 x UF-P1	2.0**	0.2*	2.2**	2.2**	0.0	-2.4**
UF-P3 x UF-P1	2.2**	-0.1	0.6	0.3	0.2	-0.4
UF-P3 x UF-P2	2.5**	0.2*	-3.2**	-3.0**	0.5*	3.9**
UF-P4 x UF-P1	2.6**	0.4**	0.1	-0.1	0.4	-0.8
UF-P4 x UF-P2	2.6**	0.0	-0.8	-1.0*	0.2	2.1
UF-P4 x UF-P3	2.7**	0.2*	0.4	0.2	-0.1	-2.6**

*, ** Denote significance at the 0.05 and 0.01 probability levels, respectively.

effects (d, aa, ad, and dd), were significant less frequent than additivity (Tables 2-10, 2-11, and 2-12). This suggests that most segregating genes for the components of resistance exhibited little dominance or digenic epistasis (interaction between two loci). However, the relative magnitude of the additive effects to the mean effects was small for all the components, suggesting that environmental variance may have influenced measurements of the components. Robinson and Comstock (1955) also suggested that estimates of additive genetic variance may be biased due to genotype x environment interactions. The predominance of additivity in the components studied should make incorporation of those genes into agronomically useful peanut lines feasible because genes for a susceptible or resistant disease reaction would not be masked (Hallauer and Miranda, 1981) by other dominant or epistatic alleles.

This study has shown that additive gene action is of major importance in controlling the components of resistance to late leafspot. Results from this study also indicate that selection for improved resistance based on these components is possible. However, the selection would be dependent on the sensitivity of the host-pathogen interaction as influenced by changes in environmental conditions. Also, there is a possibility that non-additive types of gene action may be important in some specific crosses. Because of the host-pathogen interaction with the environment (Mullaney et al.,

1982), selection of genotypes based on the replicated progeny performance would most likely provide maximum genetic progress.

Narrow-sense and Realized Heritability Estimates

Parent-offspring regression analysis was done using the F_1, F_2, and F_3 data collected from twelve crosses in both the field and greenhouse studies to obtain narrow-sense (h^2) and realized (H_R) heritability estimates. The narrow-sense and realized heritability estimates obtained are presented in Table 2-13.

Both narrow-sense and realized heritability estimates were relatively high, particularly for LP and LD; those for SP were moderate. In general, the realized heritability estimates were higher than the narrow-sense heritability estimates (Table 2-13).

The high heritability estimates on the components further substantiate the additivity obtained from the generation means analysis. These results agree with those reported by Anderson et al. (1986). In a crossing study with four C. personatum and four C. arachidicola resistant parents, Anderson et al. (1986) reported heritabilities ranging from 0.40 to 0.80 for all components of resistance (lesion no./100 cm^2 of leaf, average lesion size (mm), necrotic area, sporulation rating, and latent period) to both early and late leafspot in F_2 generation.

Table 2-13. Narrow-sense (h^2) and realized (H_R) heritability estimates for three components of resistance to late leafspot measured on twelve peanut crosses in field and greenhouse studies conducted at Gainesville, Florida, during the summers of 1989 and 1990 and in Malawi, during the 1990/91 growing season.

Location and year	Component[a]	Narrow-sense heritability	Realized heritability
Gainesville field study F_1, F_2 (1989 and 1990)	LP	0.50**	-
	LD	0.36*	-
	SP	0.33	-
Malawi field study F_2, F_3 (1990/91)	LP	0.66**	0.72**
	LD	0.62**	0.69**
	SP	0.49*	0.52**
Malawi g/house study F_2, F_3 (1990/91)	LP	0.64**	0.68**
	LD	0.57**	0.62**
	SP	0.28	0.51*
Malawi g/house and field studies F_2, F_3 (1990/91)	LP	0.59**	0.65**
	LD	0.54*	0.60**
	SP	0.43*	0.49*
Gainesville, Malawi field studies F_2, F_3 (1990/91)	LP	0.60**	0.70**
	LD	0.50**	0.62**
	SP	0.49*	0.51**
Gainesville field and Malawi g/house studies F_2, F_3 (1990/91)	LP	0.60**	0.69**
	LD	0.52**	0.61**
	SP	0.44*	0.50*

*, ** Denote significance at the 0.05 and 0.01 probability levels, respectively.

[a] LP = measurement in days, LD = measurement in mm, and SP = leafspot rating on a 1-5 scale.

In contrast, Jogloy et al. (1987) reported consistently low narrow-sense heritability estimates (0.0-0.128) for all parameters measured in F_2 and F_3 generations. Their results suggested that selection of superior plants would be ineffective in the F_2 generation, therefore, selection for resistance to C. personatum should be done in advanced generations. However, they attributed the low heritability estimates to the low number of leaves evaluated. They speculated that multiple samples may have given better estimates of individual plant resistance.

It is conceivable that estimated heritability by parent-offspring regression (Fernandez and Miller, 1985) can be confounded by either environment or interaction of genotype and environment. In this study data were collected on multiple samples from genotypes replicated over years and environments. Hence, the heritability estimates presented in this study (Table 2-13) represent better heritability estimates for the three components evaluated than those reported in the literature. Although the heritability estimates obtained from data collected from the progeny evaluated in two environments (field and greenhouse combined) were lower than those from single environments (either field or greenhouse), they are still higher than those reported by Jogloy et al. (1987).

The results of this study support previous assertions that efficient selection can be made in early generations to

develop peanut breeding lines with increased latent period, decreased lesion diameter, and reduced sporulation. This should be possible because this study has demonstrated that these components (latent period, lesion diameter, and amount of sporulation) are controlled by additive gene effects and have moderately high narrow-sense heritability estimates. Furthermore, the study has also shown that these components are quantitatively inherited.

CHAPTER 3
GENERAL COMBINING ABILITY FOR COMPONENTS OF RESISTANCE: LATENT PERIOD, LESION DIAMETER, AND AMOUNT OF SPORULATION TO LATE LEAFSPOT IN PEANUT

Introduction

Cercospora leafspot, caused by Cercospora arachidicola Hori and Cercosporidium personatum [(Berk. and Curt.) Deighton] is a major constraint to high yields of peanut (Arachis hypogaea L.). The pathogens causing this disease are distributed throughout the peanut growing areas of the world (Woodroof, 1933). Peanut farmers in many developing countries cannot afford fungicides to control this disease. Even in areas where chemical control is practiced, millions of dollars are spent annually to control the pathogens (Jackson and Bell, 1969; Porter et al., 1982; Smith, 1984). Under these circumstances, host plant resistance is a valuable tool in disease management programs.

Unfortunately, complete resistance to either pathogen has not been reported in the cultivated peanut. Nevertheless, high levels of resistance have been reported in wild Arachis species (Company et al., 1982; Foster et al., 1981), but the incorporation of those genes for resistance into the cultivated peanut is difficult.

In recent years, partial resistance has been used to develop cultivars resistant to leafspot. Partial resistance is defined as resistance that reduces the rate of an epidemic (Green and Wynne, 1986). Generally, partial resistance is governed by many genes and is therefore considered to be more durable against adaptation by the pathogen population. Incorporation of genes for resistance from germplasm with partial resistance in the cultivated peanut (Chiteka, 1987; Gorbet et al., 1987, 1990; Subrahmanyam et al., 1982) would be valuable in a disease resistance breeding program. Southern Runner, a peanut cultivar with partial resistance to late leafspot, has been released by the University of Florida (Gorbet et al., 1986). In order to efficiently exploit these sources of resistance, a thorough understanding of the genetic control of resistance is vital.

In a combining ability analysis for leafspot resistance and agronomic traits in peanut, Hamid et al. (1981) reported that variation attributable to general combining ability (GCA) was about two to five times greater than that for specific combining ability (SCA). Walls et al. (1985) observed that contribution of GCA was five times greater than SCA for components of resistance like lesion number, lesion area, defoliation, and latent period, indicating additive gene action for resistance. Anderson et al. (1986) reported highly significant GCA for all parameters of resistance to C. personatum measured in the greenhouse. Specific combining

ability was not significant for any parameter, suggesting that additive genetic variance accounted for the largest portion of the variability. Green and Wynne (1986) also reported GCA to be of greater significance in a diallel and generation means analysis for components of resistance to C. arachidicola in peanut, although large ratios of SCA/GCA sums of squares suggested the importance of non-additive genetic variance as well. These findings concur with those reported by Hamid et al. (1981) and by Kornegay et al. (1980) for resistance to early and late leafspot.

If the components of resistance to C. personatum are controlled by genes with additive or additive types of epistatic effects, efficient selection should be possible for resistant genotypes from crosses between parents of good agronomic traits and parents with leafspot resistance. Consequently, it should be feasible to increase resistance in the peanut through conventional breeding methods.

The objectives of this study were 1) to estimate combining abilities for three components of resistance to late leafspot from four peanut breeding lines and 2) to identify the best cross combination to be used in a late leafspot resistance breeding program.

Materials and Methods

Four genotypes of peanut were crossed in the greenhouse at the University of Florida, Gainesville, during the summer of 1988 in a full diallel, producing twelve F_1 cross

combinations. Criteria for selecting these genotypes were given in Table 2-1. The F_1 seed were harvested upon reaching physiological maturity and dried during spring of 1989. The F_1 plants, parents, and subsequent F_2 and F_3 plants were evaluated for three components of resistance, latent period, lesion diameter, and amount of sporulation. F_1 and F_2 plants were evaluated at the University of Florida Agronomy Farm near Gainesville, during the summers of 1989 and 1990. Some of the F_2 and F_3 were evaluated in Malawi, Africa, for the same components during the 1990/91 growing season.

Preparation of Inoculum

Cultures of C. personatum originating from diseased peanut plants were maintained in the greenhouse at the University of Florida (UF), Gainesville, Florida, USA and at the Chitedze Research Station, Lilongwe, Malawi, Africa, for the UF and Malawi studies, respectively. Cultures for the UF study were raised on the cultivar Early Bunch and cultures for the Malawi studies were raised on a susceptible cultivar, Malimba. At each site, approximately four days prior to inoculation, diseased leaves of the inoculum source were detached and placed on moist paper towels in plastic bags. The sample bags were placed in large plastic bags and incubated at room temperature. Nearly 72 h later, conidia were collected from the leaves into small test tubes using a cyclone spore collector attached to a vacuum pump. A hemacytometer was used to measure the concentration of the

conidial suspension and then diluted to 5000 conidia/mL. This concentration was used based on an earlier study (Chiteka, 1987). One drop of Tween 80/100 mL of conidia suspension was added as a surfactant.

F_1 Field Study

Ten F_1 seed from each cross were pre-germinated in small jiffy pots in the greenhouse prior to planting. Remaining F_1 seed were kept for further studies. The F_1 plants were transplanted to the field on 14 April 1989 at the UF Agronomy Farm, near Gainesville. Seed of the parental lines were planted at the same time. The plants were grown in single rows, 3.0 m long spaced 0.91 m apart. The spacing between plants was 30 cm, and each row had ten plants. The field was isolated from other peanut fields and had not been planted to peanut the previous two years. The isolation and early date of planting reduced the probability that external inoculum might have interfered with data collection, especially on latent period (measured as number of days from inoculation to first sporulating lesion). Standard cultural practices for peanut in Florida were followed (Whitty et al., 1975). However, fungicides were not applied.

Three target tetrafoliolate leaves from five randomly selected plants from each cross were tagged. Approximately 35 d after planting, the three tetrafoliolate leaves were artificially inoculated with CP conidia. Inoculations were made with a Spra Tool (Fisher Scientific Products, Pittsburgh,

PA) calibrated to deliver 1 mL of inoculum per tetrafoliolate leaf. Each target leaf was held flat on a wooden board and the adaxial surface sprayed with the spore suspension for one second. The inoculated leaves were used to monitor components of resistance to late leafspot. The target leaves were examined every other day beginning five days after inoculation for 35-40 d. Data were collected on the following components of resistance:

1) latent period (LP)--measured as number of days from inoculation to first sporulating lesion,

2) lesion diameter (LD)--mean diameter (mm) of two lesions randomly selected for each target tetrafoliolate leaf,

3) amount of sporulation (SP)--amount of sporulation based on a 1-5 scale, according to Subrahmanyam et al. (1982), where 1 = little or no sporulation, 5 = profuse sporulation.

F_2 Field Study

Half of the selfed seed from the F_1 field study and seed of the parental lines were also planted during the summer of 1990 at the UF Agronomy Farm. The seed were planted in rows 0.91 m apart with 30 cm intrarow spacings. A randomized complete block design with two replications was used. Target tetrafoliolate leaves from the selected plants were inoculated with CP conidia as described for the F_1 field study. Data were collected on the components of resistance. The remaining half of the seed from 1989 and F_3 seed from the 1990 field studies were planted in Malawi during the 1990/91 growing

season.

F_2 and F_3 Field and Greenhouse Studies

Two field experiments and one greenhouse study were carried out in Malawi during the 1990/91 growing season. One field experiment was conducted at the Chitala experimental station and the other at the Kasinthula experimental station. The greenhouse study was conducted at the Chitedze Research Station. Seed for the field experiments were planted on two ridges, 6.0 m long, spaced 0.91 m apart and 30 cm between plants within rows. A randomized complete block design with three replications was used at both sites. Five plants from each cross were randomly selected from each experiment to be inoculated with CP. Three tetrafoliolate leaves were tagged and inoculated with CP conidia following the procedure described for the F_1 field study at Gainesville. Cultural practices for peanut production in Malawi (Chiyembekeza and Sibale, 1986) were followed.

Seed for the greenhouse study were planted in 15 cm diameter pots. The pots were arranged on a greenhouse bench in a randomized complete block design, replicated three times. Three pots were utilized per genotype and per replication. Inoculation was carried out in the same manner as for the F_1 field study. The inoculated plants were placed in a mist chamber as described by Chiteka (1987). Data were collected on the three components of resistance.

Statistical Analysis

Analysis of variance (ANOVA) procedure (SAS, 1988) was performed on data from each study for each component. The least significance difference (LSD) mean separation procedure was used to compare the entry means.

Diallel analysis for reciprocal cross differences and combining ability was carried out following Griffing (1956a) Method 1 Model I. A SAS Macro GRIFFING program, implementing Griffing's Analysis of Diallel Crossing Systems, developed by Stephen B. Linda (IFAS Consulting Division, Department of Statistics, University of Florida) was utilized. The error degrees of freedom (df) from the ANOVA for each study were used in the SAS Macro GRIFFING program to generate mean squares for GCA, SCA, and reciprocal effects. General, specific, and reciprocal combining ability effects were computed for each parent for the three components of resistance.

To determine the magnitude of GCA effects, ratios of GCA/SCA mean squares were computed. The expectations of mean squares for the analysis of variance for Method 1 with the assumptions of Model I for this study were calculated according to assumptions of Model I described in Table 3-1.

Results and Discussion

F_1 and F_2 Field Studies at Gainesville

Latent period, lesion diameter, and amount of sporulation were reported (Chiteka et al., 1988) to be repeatable

Table 3-1. Analysis of variance for Method 1 giving generalized expectations of mean squares for assumptions of Model I.

Source	df	Sum of squares	Mean squares	Expectations of mean squares
GCA	3	S_g	M_g	$\sigma^2 + 2.64\Sigma g_i^2$
SCA	6	S_s	M_s	$\sigma^2 + 0.17\Sigma\Sigma s_{ij}^2$
Reciprocal effects	6	S_r	M_r	$\sigma^2 + 0.34\Sigma\Sigma r_{ij}^2$
Error	m	S_e	M_e'	σ^2

components of partial resistance to late leafspot in peanut. Genotypes with longer latent period, small lesion size, and reduced sporulation, exhibit this type of resistance. Parlevliet (1979) asserted that several components contribute to the reduction of the rate of an epidemic, the most important being 1) reduction in infection frequency or lesion number, 2) lengthening of latent period, and 3) a decrease in sporulation.

Overall means of the components of resistance measured in F_1 and F_2 generations in the field study conducted at Gainesville in 1990 are presented as diallel table of means in Tables 3-2 and 3-3, respectively. Measurements of each component were the average of the number of observations within each replicate for the crosses and parents.

The measurements of latent period (LP) on the F_1 generation ranged between 24.9 and 33.3 d. Measurements of lesion diameter (LD) ranged from 1.7 to 2.6 mm; those for amount of sporulation (SP) ranged from 1.7 to 2.7 (Table 3-2). LP measurements on the F_2 generation ranged between 21.7 and 32.3 d. Measurements of LD ranged from 1.3 to 2.4 mm and measurements of SP ranged from 1.8 to 2.7 (Table 3-3). Genotype UF-P1 and UF-P3 had the longest LP as compared with UF-P2 and UF-P4; lesion diameter and amount of sporulation measurements were low for UF-P1 and UF-P2. Genotype UF-P3 had significantly smaller LD and SP compared to the other three genotypes. The overall ranking of the genotypes for the three

Table 3-2. Diallel table of means for latent period (LP), lesion diameter (LD), and amount of sporulation (SP) measured in F_1 generation for crosses and parents in the field study conducted at Gainesville, Florida, 1990.

Female Parent	Component[a]	Male Parent UF-P1	UF-P2	UF-P3	UF-P4	Mean
UF-P1	LP	30.4	26.9	27.0	27.1	27.9
	LD	2.3	2.6	1.9	2.2	2.3
	SP	2.4	2.6	2.0	2.5	2.4
UF-P2	LP	31.6	27.5	30.7	24.9	28.7
	LD	2.0	2.3	2.0	2.4	2.2
	SP	2.3	2.2	2.1	2.7	2.3
UF-P3	LP	27.7	33.3	32.8	26.5	30.1
	LD	2.1	1.7	1.8	1.9	1.9
	SP	2.4	1.7	1.8	2.0	2.0
UF-P4	LP	27.5	29.6	32.2	25.7	28.8
	LD	2.4	2.0	1.9	2.4	2.2
	SP	2.4	2.5	2.2	2.6	2.4
Mean	LP	29.3	29.3	30.7	26.1	28.9
	LD	2.2	2.2	1.9	2.2	2.1
	SP	2.4	2.3	2.0	2.5	2.3

LSD (P=.05) for means: LP = 2.1 LD = 0.2 SP = 0.3

[a] LP = measurement in days, LD = measurement in mm, and SP = leafspot rating on a 1-5 scale.

Table 3-3. Diallel table of means for latent period (LP), lesion diameter (LD), and amount of sporulation (SP) measured in F_2 generation for crosses and parents in the field study conducted at Gainesville, Florida, 1990.

Female Parent	Component[a]	Male Parent UF-P1	UF-P2	UF-P3	UF-P4	Mean
UF-P1	LP	28.0	29.0	29.0	25.3	27.8
	LD	2.2	2.3	1.3	2.2	2.0
	SP	2.3	2.3	2.0	2.4	2.3
UF-P2	LP	28.8	28.1	31.7	21.7	27.6
	LD	1.8	2.3	1.8	2.3	2.1
	SP	2.0	2.3	2.2	2.7	2.3
UF-P3	LP	32.3	27.1	31.9	24.7	29.0
	LD	2.1	2.1	1.8	2.3	2.1
	SP	2.2	2.5	1.8	2.2	2.2
UF-P4	LP	29.4	27.0	29.9	25.0	27.8
	LD	2.4	2.3	1.7	2.3	2.2
	SP	2.6	2.6	2.1	2.3	2.4
Mean	LP	29.6	27.8	30.6	24.2	28.1
	LD	2.1	2.3	1.7	2.3	2.1
	SP	2.3	2.4	2.0	2.4	2.3

LSD (P=.05) for means: LP = 2.9 LD = 0.3 SP = 0.4

[a] LP = measurement in days, LD = measurement in mm, and SP = leafspot rating on a 1-5 scale.

components from high to low was UF-P3, UF-P1, UF-P2, and UF-P4. In general, crosses involving UF-P1 and UF-P3 either as male or female parent resulted in increased LP and reduced LD and SP. Almost all crosses involving UF-P4 gave shorter LP and increased LD and SP (Table 3-2 and 3-3). Results on the performance of parental genotypes, UF-P1, UF-P2, UF-P3, and UF-P4 concur with those reported by Chiteka (1987).

Data from parental lines, F_1, and F_2 generations (Table 3-2 and Table 3-3) were subjected to diallel analysis following Method 1 Model I of Griffing (1956a). The sources of variation were partitioned into general, specific, and reciprocal effects. Mean squares for general, specific, and reciprocal effects from the analysis are presented in Table 3-4.

Mean squares for GCA, SCA, and reciprocal effects were significant for the three components of resistance measured. Nonetheless, the mean squares attributable to GCA effects were greater than for SCA and for reciprocal effects for all the components (Table 3-4). This demonstrates that GCA accounted for the largest variation, suggesting that additive genetic effects were important for these components. Other workers (Anderson et al., 1986; Hamid et al., 1981; Walls and Wynne, 1985) have reported similar results.

In general, three genotypes: UF-P1, UF-P2, and UF-P3 consistently produced progeny with long LP, small LD, and reduced SP when used in crosses as female parents. This trend

was consistent in both the F_1 and the F_2 generation (Table 3-2 and 3-3), suggesting some cytoplasmic genetic effects from the female parent.

Reciprocal cross differences were also noticed in certain crosses, particularly those involving genotype UF-P3. Although genotype UF-P4 is susceptible to CP, in crosses where UF-P3 was used as a male parent, the resultant progeny had long LP, small LD, and reduced SP (Table 3-2 and 3-3), suggesting a paternal effect from this genotype. Thus, in a late leafspot resistance breeding program involving utilization of both resistant and susceptible genotypes, it would be advisable to use UF-P3 as female parent when intercrossed with another resistant genotype. On the other hand, when a susceptible parent is utilized in the program, it would be advisable to use UF-P3 as a male parent. Coffelt and Porter (1986) reported similar results in field screening tests of reciprocal peanut populations of Chico x Florigiant for resistance to leafspot. They attributed the differences in susceptibility to leafspot from the reciprocal cross populations to cytoplasmic and additive effects and argued that those effects may control leafspot resistance.

Means of the parental lines for each component, averaged over crosses (Tables 3-2 and 3-3) were used to compute GCA effects for each parent. The magnitude of the estimated GCA effects for each component indicates the relative importance of a parent in a cross combination. Large positive GCA

Table 3-4. Mean squares for general and specific combining abilities for three components of resistance to late leafspot measured on F_1 and F_2 generations in the field study conducted at Gainesville, Florida, 1990.

Source	df	Latent period (days)	Lesion diameter (mm)	Sporulation score (1-5 scale)
		F_1 generation		
GCA	3	21.49**	0.18**	0.29**
SCA	6	3.73*	0.02**	0.02**
Reciprocal	6	4.87**	0.05*	0.04*
Error	448	0.160	0.001	0.001
		F_2 generation		
GCA	3	26.31**	0.06**	0.11**
SCA	6	3.10*	0.02*	0.06*
Reciprocal	6	5.86*	0.02**	0.03**
Error	448	0.160	0.001	0.001

*,** Denote significance at the 0.05 and 0.01 probability levels, respectively.

effects are desirable for latent period; large negative values for GCA effects are, on the other hand, desirable for lesion diameter and amount of sporulation.

Estimates computed for GCA effects on the three components of resistance, LP, LD, and SP are presented in Table 3-5. The three components were measured on F_1 and F_2 generations in the field studies conducted at Gainesville in the summer of 1989 and 1990, respectively. In the F_1 generation, genotype UF-P3 gave the largest positive GCA effects for LP and the largest negative GCA effects for lesion diameter and amount of sporulation (Table 3-5). The estimate of GCA effects for LP was 2.34; the estimate for LD was -0.22 and that for SP was -0.27.

Genotype UF-P3, also had the largest positive GCA effects in the F_2 generation for LP and the largest negative GCA effects for LD and SP. In the F_2 generation, the GCA value for UF-P3 on LP was 1.05; the value for LD was -0.10 and that for SP was -0.13. Genotype UF-P1 had a positive GCA value for LP and negative values for LD and SP. For genotype UF-P1, the GCA value for LP was 0.42; the GCA value for LD was -0.01 and that for SP was -0.03. Genotype UF-P4 gave the largest negative GCA values for LP and largest positive GCA values for LD and SP in both the F_1 and the F_2 generations (Table 3-5), indicating susceptibility to late leafspot.

The ranking of the parental means for the components agrees with the ranking according to the GCA effects. This

Table 3-5. Estimates of general combining ability (GCA) effects for three components of resistance to late leafspot measured on F_1 and F_2 generations in the field study conducted at Gainesville, Florida, 1990.

Parent	Latent period (days)	Lesion diameter (mm)	Sporulation score (1-5 scale)
		F_1 generation	
UF-P1	-0.45	0.11	0.08
UF-P2	-0.40	0.02	0.02
UF-P3	2.34	-0.22	-0.27
UF-P4	-1.49	0.09	0.17
S.E.(g_i)[1]	1.39	0.13	0.16
		F_2 generation	
UF-P1	0.42	-0.01	-0.03
UF-P2	-0.67	0.01	0.02
UF-P3	1.05	-0.10	-0.13
UF-P4	-0.80	0.10	0.15
S.E.(g_i)	0.75	0.07	0.10

[1] Standard error of the GCA effects

indicates that selection of parents based on parental performance may result in the best possible crosses for increased latent period, reduced lesion diameter, and decreased amount of sporulation.

To determine whether dominance effects played a role in inheritance of the three components of resistance, specific combining ability effects were computed for each cross (Hayman, 1958). Results of the estimates of SCA effects are given in Table 3-6 and Table 3-7.

The SCA effects of UF-P1, UF-P2, and UF-P3 indicated that these parents transmit desirable genes uniformly to all their hybrids for increased latent period, reduced lesion diameter, and decreased amount of sporulation. The following crosses: UF-P3 x UF-P1, UF-P2 x UF-P3, and UF-P3 x UF-P4 gave the best combination for increased LP, reduced LD, and decreased amount of sporulation in the F_1 generation; cross UF-P1 x UF-P2 and UF-P2 x UF-P3 gave the best combination for the same components in the F_2 generation. Performance of the crosses was consistent over generations. Reciprocal cross differences were noticed, particularly in the crosses involving UF-P2 and UF-P3. Thus, even though UF-P2 appears more susceptible to CP than UF-P3, a high level of resistance is obtained from the crosses in the F_2, F_3, and possibly in later generations.

F_2 and F_3 Field Studies in Malawi

Combined analysis for the field studies conducted in Malawi showed no significant genotype by location interaction.

Table 3-6. Estimates of specific combining ability (SCA) effects on latent period (LP), lesion diameter (LD), and amount of sporulation (SP) measured on F_1 generation in the field study conducted at Gainesville, Florida, 1990.

		Male Parent			
Female Parent	Component[a]	UF-P1	UF-P2	UF-P3	UF-P4
UF-P1	LP	-	0.70	-2.46	-0.15
	LD	-	0.04	0.03	-0.01
	SP	-	0.06	0.10	-0.09
UF-P2	LP	-2.34	-	0.66	-0.25
	LD	0.28	-	-0.07	-0.09
	SP	0.11	-	-0.09	0.11
UF-P3	LP	1.14	-1.28	-	1.11
	LD	-0.10	0.16	-	-0.07
	SP	-0.24	0.21	-	-0.05
UF-P4	LP	-0.19	-2.35	-0.84	-
	LD	-0.07	0.13	0.02	-
	SP	0.06	0.08	-0.10	-
S.E.(s_{ij})[1]					
	LP	1.08			
	LD	0.07			
	SP	0.08			
S.E.(r_{ij})[2]					
	LP	1.56			
	LD	0.15			
	SP	0.15			

[a] LP = measurement in days, LD = measurement in mm, and SP = leafspot rating on a 1-5 scale.
[1] Standard error of the normal crosses
[2] Standard error of the reciprocal crosses

Table 3-7. Estimates of specific combining ability (SCA) effects on latent period (LP), lesion diameter (LD), and amount of sporulation (SP) measured on F_2 generation in the field study conducted at Gainesville, Florida, 1990.

		Male Parent			
Female Parent	Component[a]	UF-P1	UF-P2	UF-P3	UF-P4
UF-P1	LP	-	2.87	-1.63	-0.36
	LD	-	-0.12	0.12	-0.01
	SP	-	-0.16	0.10	0.06
UF-P2	LP	-1.65	-	-0.41	-0.74
	LD	0.22	-	-0.02	0.04
	SP	0.12	-	0.11	0.16
UF-P3	LP	-0.90	-0.10	-	0.49
	LD	0.06	-0.03	-	0.09
	SP	0.11	-0.11	-	0.09
UF-P4	LP	-2.05	-1.12	2.93	-
	LD	-0.12	0.02	0.02	-
	SP	-0.11	0.07	-0.20	-
S.E.(s_{ij})[1]					
	LP	1.26			
	LD	0.09			
	SP	0.14			
S.E.(r_{ij})[2]					
	LP	1.71			
	LD	0.11			
	SP	0.13			

[a] LP = measurement in days, LD = measurement in mm, and SP = leafspot rating on a 1-5 scale.
[1] Standard error of the normal crosses
[2] Standard error of the reciprocal crosses

Hence, results for the two studies conducted at Chitala experimental station and at Kasinthula experimental station are presented and discussed together. Means of the components of resistance measured in F_2 and F_3 generations for the crosses and parents are presented in Tables 3-8 and 3-9. Measurements of LP from the F_2 generation averaged over replications, ranged from 23.9 to 31.1 d. Mean measurements of LD ranged between 1.2 and 2.7 mm while measurements of SP ranged from 1.7 to 2.9 (Table 3-8).

Mean measurements of LP taken on the F_3 generation, also ranged from 23.9 to 31.1 d; measurements of LD ranged between 1.2 and 2.3 mm, and measurements of SP ranged from 1.7 to 2.9 (Table 3-9). In these studies, genotype UF-P3 had the longest LP while UF-P4 had the shortest LP. Likewise, UF-P3 gave the smallest LD and the least sporulation while UF-P4 had the largest LD and greatest sporulation. Crosses involving UF-P1, UF-P2, and UF-P3 either as male or female parents produced progeny with increased LP and reduced LD and decreased SP. Almost all crosses involving UF-P4 produced progeny with low LP and increased LD and SP (Table 3-8 and 3-9). These results concur with those obtained at Gainesville, 1990 and those reported by Chiteka (1987) on the same genotypes.

Mean squares for general, specific, and reciprocal effects from the analysis of variance are given in Table 3-10. GCA, SCA, and reciprocal mean squares were significant for the three components of resistance. However, mean squares

Table 3-8. Diallel table of means for latent period (LP), lesion diameter (LD), and amount of sporulation (SP) measured in F_2 generation for crosses and parents in the field study conducted in Malawi, during the 1990/91 growing season.

Female Parent	Component[a]	Male Parent UF-P1	UF-P2	UF-P3	UF-P4	Mean
UF-P1	LP	26.5	26.7	27.4	25.1	26.4
	LD	1.5	1.3	1.5	2.1	1.6
	SP	1.7	2.0	1.8	1.9	1.9
UF-P2	LP	26.0	26.0	29.0	26.9	27.0
	LD	1.5	1.8	1.3	2.7	1.8
	SP	1.8	2.2	1.9	2.3	2.1
UF-P3	LP	26.6	27.9	31.1	26.4	28.0
	LD	1.4	1.4	1.2	1.6	1.4
	SP	1.9	1.8	1.7	2.1	1.9
UF-P4	LP	26.6	25.6	26.7	23.9	25.7
	LD	2.0	2.1	1.6	2.3	2.0
	SP	2.4	2.1	2.1	2.9	2.4
Mean	LP	26.4	26.6	28.6	25.6	26.8
	LD	1.7	1.7	1.5	2.3	1.8
	SP	1.9	2.0	1.8	2.2	2.0

LSD (P=.05) for means: LP = 1.2 LD = 0.2 SP = 0.2

[a] LP = measurement in days, LD = measurement in mm, and SP = leafspot rating on a 1-5 scale.

Table 3-9. Diallel table of means for latent period (LP), lesion diameter (LD), and amount of sporulation (SP) measured in F_3 generation for crosses and parents in the field study conducted in Malawi, during the 1990/91 growing season.

Female Parent	Component[a]	Male Parent UF-P1	UF-P2	UF-P3	UF-P4	Mean
UF-P1	LP	26.5	28.2	27.7	24.4	26.7
	LD	1.5	1.4	1.2	1.9	1.5
	SP	1.7	1.8	1.8	1.9	1.8
UF-P2	LP	26.3	26.0	26.1	26.4	26.2
	LD	1.7	1.8	1.5	1.9	1.7
	SP	1.8	2.2	1.8	1.9	1.9
UF-P3	LP	25.9	27.1	31.1	25.6	27.4
	LD	1.3	1.5	1.2	1.6	1.4
	SP	2.0	1.8	1.7	1.9	1.9
UF-P4	LP	25.2	24.7	26.3	23.9	25.0
	LD	2.2	2.1	2.3	2.3	2.2
	SP	2.2	2.1	2.3	2.9	2.4
Mean	LP	26.0	26.5	27.8	25.1	26.3
	LD	1.9	2.0	1.9	2.0	2.0
	SP	1.7	1.7	1.6	2.1	1.8

LSD (P=.05) for means: LP = 1.1 LD = 0.2 SP = 0.2

[a] LP = measurement in days, LD = measurement in mm, and SP = leafspot rating on a 1-5 scale.

attributable to GCA effects were greater than those for SCA and for reciprocal effects. This was true for all the components in both F_2 and F_3 generations (Table 3-10).

Means of the parental lines averaged over crosses and replicates (Tables 3-8 and 3-9) were used to compute GCA effects for each parent. The computed values for GCA effects for the three components of resistance are presented in Table 3-11.

In both field studies involving the F_2 and the F_3 generation material conducted in Malawi, UF-P3 gave greatest GCA effects for latent period, lesion diameter, and amount of sporulation (Table 3-11). The GCA values for LP were 1.60 for the F_2 generation and 1.59 for the F_3 generation. Values of GCA effects for LD were -0.10 for the F_2 generation and -0.08 for the F_3 generation; GCA values for SP were -0.36 for the F_2 generation and -0.27 for the F_3 generation. Genotype UF-P4 gave the largest negative GCA values for LP and the largest positive GCA values for LD and SP (Table 3-11), indicating lack of partial resistance.

Estimates of SCA effects for the three components of resistance are given in Table 3-12 and Table 3-13. SCA effects for UF-P1, UF-P2, and UF-P3, also indicated that these parents favorably combined genes for increased latent period, reduced lesion diameter, and decreased amount of sporulation. Thus, selection of desirable segregants for late leafspot resistance would be possible. These crosses: UF-P1 x UF-P2,

Table 3-10. Mean squares for general and specific combining abilities for three components of resistance to late leafspot measured on F_2 and F_3 generations in the field studies conducted in Malawi, during the 1990/91 growing season.

Source	df	Latent period (days)	Lesion diameter (mm)	Sporulation score (1-5 scale)
			F_2 generation	
GCA	3	10.42**	0.10**	1.13**
SCA	6	3.05**	0.01*	0.05**
Reciprocal	6	0.41**	0.01*	0.05*
Error	384	0.0400	0.0003	0.0007
			F_3 generation	
GCA	3	12.93**	0.11**	0.84**
SCA	6	3.56**	0.02*	0.02*
Reciprocal	6	1.00*	0.03**	0.05**
Error	384	0.0100	0.0001	0.0006

*,** Denote significance at the 0.05 and 0.01 probability levels, respectively.

Table 3-11. Estimates of general combining ability (GCA) effects for three components of resistance to late leafspot on four parental peanut genotypes measured in F_2 and F_3 generations in the field studies conducted in Malawi, during the 1990/91 growing season.

Parent	Latent period (days)	Lesion diameter (mm)	Sporulation score (1-5 scale)
		F_2 generation	
UF-P1	-0.33	-0.09	-0.14
UF-P2	-0.18	0.06	-0.03
UF-P3	1.60	-0.10	-0.36
UF-P4	-1.10	0.13	0.53
S.E.(g_i)[1]	0.97	0.09	0.32
		F_3 generation	
UF-P1	-0.11	-0.07	-0.17
UF-P2	-0.03	-0.01	-0.03
UF-P3	1.59	-0.08	-0.27
UF-P4	-1.45	0.17	0.46
S.E.(g_i)	1.08	0.10	0.27

[1] Standard error of the GCA effects

UF-P2 x UF-P3, and UF-P2 x UF-P1 gave the best combination for increased LP, reduced LD, and decreased amount of sporulation in the F_2 generation; also, crosses UF-P1 x UF-P2, UF-P3 x UF-P1, and UF-P2 x UF-P3 gave the best combination for the same components in the F_3 generation. Reciprocal cross differences were also noticed in these crosses.

F_2 and F_3 Greenhouse Study Conducted in Malawi

The greenhouse study conducted in Malawi during the 1990/1991 growing season, provided additional information on the performance of the four genotypes and the crosses under a controlled environment. Both F_2 and F_3 material and the four parental lines were evaluated for the three components of resistance. Diallel means of measurements on the components of resistance for the F_2 and F_3 generations are presented in Table 3-14 and Table 3-15, respectively.

Significant differences ($P< 0.05$) were observed among the means of the four parental lines and the twelve crosses for the three components. Measurements of LP from the F_2 generation ranged from 25.0 to 31.3 d. Mean measurements of LD ranged between 1.0 and 1.8 mm while measurements of SP ranged from 1.1 to 3.1 (Table 3-14).

Mean measurements of LP taken on the F_3 generation ranged from 25.2 to 31.3 d; measurements of LD ranged between 1.1 and 1.9 mm and measurements of SP ranged from 1.1 to 3.0 (Table 3-15). In this study, UF-P3 had the longest LP while UF-P4 had the shortest LP. Likewise, UF-P3 gave the smallest

Table 3-12. Estimates of specific combining ability (SCA) effects on latent period (LP), lesion diameter (LD), and amount of sporulation (SP) measured on F_2 generation in the field studies conducted in Malawi, during the 1990/91 season.

Female Parent	Component[a]	Male Parent UF-P1	UF-P2	UF-P3	UF-P4
UF-P1	LP	-	0.35	-1.78	0.77
	LD	-	-0.02	0.10	-0.04
	SP	-	-0.19	0.12	0.10
UF-P2	LP	0.34	-	0.45	0.28
	LD	-0.07	-	-0.04	-0.05
	SP	-0.10	-	-0.04	0.12
UF-P3	LP	-0.57	-0.48	-	-0.65
	LD	-0.03	0.04	-	0.03
	SP	0.05	-0.07	-	-0.23
UF-P4	LP	-0.74	-0.10	0.02	-
	LD	-0.06	0	0.06	-
	SP	-0.17	0.27	-0.15	-
S.E.(s_{ij})[1]					
	LP	0.97			
	LD	0.05			
	SP	0.12			
S.E.(r_{ij})[2]					
	LP	0.45			
	LD	0.05			
	SP	0.15			

[a] LP = measurement in days, LD = measurement in mm, and SP = leafspot rating on a 1-5 scale.
[1] Standard error of the normal crosses
[2] Standard error of the reciprocal crosses

Table 3-13. Estimates of specific combining ability (SCA) effects on latent period (LP), lesion diameter (LD), and amount of sporulation (SP) measured on F_3 generation in the field studies conducted in Malawi, during the 1990/91 growing season.

		Male Parent			
Female Parent	Component[a]	UF-P1	UF-P2	UF-P3	UF-P4
UF-P1	LP	-	0.87	-1.17	-0.15
	LD	-	-0.04	0.09	0.03
	SP	-	-0.03	-0.03	0.01
UF-P2	LP	0.98	-	1.46	0.53
	LD	-0.01	-	-0.08	-0.10
	SP	-0.12	-	0.05	0.17
UF-P3	LP	0.91	-0.47	-	-0.69
	LD	-0.10	-0.01	-	0.08
	SP	-0.06	-0.02	-	-0.02
UF-P4	LP	-0.42	0.86	-0.33	-
	LP	-0.19	-0.07	-0.21	-
	SP	-0.13	-0.10	-0.34	-
S.E.(s_{ij})[1]					
	LP	1.05			
	LD	0.08			
	SP	0.08			
S.E.(r_{ij})[2]					
	LP	0.71			
	LD	0.13			
	SP	0.16			

[a] LP = measurement in days, LD = measurement in mm, and SP = leafspot rating on a 1-5 scale.
[1] Standard error of the normal crosses
[2] Standard error of the reciprocal crosses

Table 3-14. Diallel table of means for latent period (LP), lesion diameter (LD), and amount of sporulation (SP) measured in F_2 generation for crosses and parents in the greenhouse study conducted at Chitedze Research Station, Malawi, during the 1990/91 growing season.

Female Parent	Component[a]	Male Parent UF-P1	UF-P2	UF-P3	UF-P4	Mean
UF-P1	LP	27.3	28.0	29.8	25.1	27.6
	LD	1.6	1.7	1.0	1.8	1.5
	SP	1.9	1.9	1.5	3.1	2.1
UF-P2	LP	27.6	28.0	30.4	26.0	28.0
	LD	1.7	1.6	1.4	1.8	1.6
	SP	2.4	2.1	1.6	3.4	2.4
UF-P3	LP	26.9	30.9	31.3	29.1	29.6
	LD	1.3	1.5	1.2	1.4	1.4
	SP	1.3	2.1	1.1	1.7	1.6
UF-P4	LP	26.0	27.6	28.7	25.0	26.8
	LD	1.8	1.6	1.6	1.7	1.7
	SP	2.7	2.9	1.9	3.0	2.6
Mean	LP	27.0	28.6	30.1	26.1	28.0
	LD	1.6	1.6	1.3	1.7	1.6
	SP	2.1	2.3	1.5	2.8	2.2

LSD (P=.05) for means: LP = 1.4 LD = 0.3 SP = 0.4

[a] LP = measurement in days, LD = measurement in mm, and SP = leafspot rating on a 1-5 scale.

Table 3-15. Diallel table of means for latent period (LP), lesion diameter (LD), and amount of sporulation (SP) measured in F_3 generation for crosses and parents in the greenhouse study conducted at Chitedze Research Station, Malawi, during the 1990/91 growing season.

Female Parent	Component[a]	Male Parent UF-P1	UF-P2	UF-P3	UF-P4	Mean
UF-P1	LP	27.3	27.8	30.4	25.2	27.7
	LD	1.6	1.2	1.4	1.7	1.5
	SP	1.9	1.1	1.4	1.9	1.6
UF-P2	LP	27.1	28.0	29.1	26.9	27.8
	LD	1.9	1.6	1.2	1.6	1.6
	SP	2.1	2.1	1.8	2.7	2.2
UF-P3	LP	27.4	28.6	31.3	26.0	28.3
	LD	1.1	1.8	1.1	1.6	1.4
	SP	1.7	1.7	1.2	1.9	1.6
UF-P4	LP	26.4	26.7	26.7	25.4	26.3
	LD	1.7	1.6	1.6	1.7	1.7
	SP	2.2	2.0	2.1	3.0	2.3
Mean	LP	27.1	27.8	29.4	26.0	27.5
	LD	1.7	1.5	1.4	1.7	1.6
	SP	1.8	1.8	1.6	2.3	1.9

LSD (P=.05) for means: LP = 2.9 LD = 0.3 SP = 0.4

[a] LP = measurement in days, LD = measurement in mm, and SP = leafspot rating on a 1-5 scale.

LD and the least amount of sporulation while UF-P4 gave the largest LD and most amount of sporulation. Crosses involving UF-P1, UF-P2, and UF-P3 either as male or female parents produced progeny with increased LP, reduced LD, and decreased SP.

Almost all crosses involving UF-P4 gave low LP and increased LD and SP (Table 3-14 and 3-15). These results are in agreement with those obtained in the field study at Gainesville and those from the field studies conducted in Malawi.

Mean squares for GCA, SCA, and reciprocal effects for the three components are presented in Table 3-16. The mean squares for GCA, SCA, and reciprocal effects were significant for the three components. Even though this was the case, the GCA effects were significantly higher than that of SCA or reciprocal effects in both the F_2 and the F_3 generation for the three components. These results also agree with those obtained from the field study conducted at Gainesville, 1990 and the field studies conducted in Malawi during the 1990/1991 growing season.

Means of the parental lines (Tables 3-14 and 3-15) were used to compute GCA effects for each parent. The computed GCA values for both the F_2 and the F_3 generations are presented in Table 3-17.

In this study (Table 3-17) involving both F_2 and F_3 generation material, genotype UF-P3 gave the greatest GCA

Table 3-16. Mean squares for general and specific combining abilities for three components of resistance to late leafspot measured on F_2 and F_3 generations in the greenhouse study conducted at Chitedze Research Station, Malawi, during the 1990/91 growing season.

Source	df	Latent period (days)	Lesion diameter (mm)	Sporulation score (1-5 scale)
			F_2 generation	
GCA	3	17.35**	0.07**	1.90**
SCA	6	0.99*	0.05**	0.13**
Reciprocal	6	1.68**	0.02*	0.08*
Error	384	0.0500	0.0006	0.0036
			F_3 generation	
GCA	3	17.87**	0.01**	0.98**
SCA	6	4.47*	0.04**	0.07*
Reciprocal	6	4.70*	0.06**	0.16**
Error	384	0.0700	0.0006	0.0032

*,** Denote significance at the 0.05 and 0.01 probability levels, respectively.

effects for latent period, lesion diameter, and amount of sporulation. The values of the GCA effects for LP were 2.14 for the F_2 generation and 1.08 for the F_3 generation. For the same genotype, GCA values for LD were -0.14 for the F_2 generation and -0.02 for the F_3 generation. GCA values for SP were -0.62 for the F_2 generation and -0.36 for the F_3 generation. Genotype UF-P4 gave the largest negative GCA values for LP and the largest positive GCA values for LD and SP (Table 3-17), indicating susceptibility to late leafspot.

Specific combining ability effects were also computed for each cross combination on the F_2 and the F_3 data. Estimates of the SCA effects for the three components are given in Table 3-18 and Table 3-19.

SCA effects for UF-P1, UF-P2, and UF-P3 from the greenhouse study in Malawi, also indicated that these parents nicked well for increased LP, reduced LD, and decreased SP. The following crosses: UF-P1 x UF-P2, UF-P2 x UF-P3, UF-P2 x UF-P1, UF-P3 x UF-P4, and UF-P4 x UF-P3 gave the best combination for increased LP, reduced LD, and decreased SP in the F_2 generation; crosses UF-P1 x UF-P2, UF-P2 x UF-P1, and UF-P2 x UF-P3 gave the best combination for the same components in the F_3 generation.

Mean Square Ratios for GCA and SCA

In order to quantify the significance of gene effects in these studies, the relative magnitude of mean squares (MS) for general (GCA) and specific (SCA) combining ability for the

Table 3-17. Estimates of general combining ability (GCA) effects for three components of resistance to late leafspot measured on F_2 and F_3 generations in the greenhouse study conducted at Chitedze Research Station, Malawi, during the 1990/91 growing season.

Parent	Latent period (days)	Lesion diameter (mm)	Sporulation score (1-5 scale)
		F_2 generation	
UF-P1	-0.22	0.05	-0.07
UF-P2	-0.81	0.02	0.13
UF-P3	2.14	-0.14	-0.62
UF-P4	-1.11	0.07	0.56
S.E.(g_i)[1]	1.25	0.08	0.41
		F_3 generation	
UF-P1	0.30	-0.01	-0.18
UF-P2	-0.08	0.01	0.10
UF-P3	1.08	-0.02	-0.36
UF-P4	-1.30	0.03	0.44
S.E.(g_i)	0.84	0.02	0.34

[1] Standard error of the GCA effects

Table 3-18. Estimates of specific combining ability (SCA) effects on latent period (LP), lesion diameter (LD), and amount of sporulation (SP) measured on F_2 generation in the greenhouse study conducted at Chitedze Research Station, Malawi, during the 1990/91 growing season.

			Male Parent		
Female Parent	Component[a]	UF-P1	UF-P2	UF-P3	UF-P4
UF-P1	LP	-	0.39	0.01	0.25
	LD	-	-0.01	0.01	0.10
	SP	-	-0.07	-0.07	0.27
UF-P2	LP	0.22	-	1.09	-0.50
	LD	-0.02	-	-0.13	-0.07
	SP	-0.22	-	-0.16	0.28
UF-P3	LP	-0.56	1.78	-	0.45
	LD	0.21	0.10	-	-0.02
	SP	0.07	-0.26	-	-0.28
UF-P4	LP	-0.22	0	1.22	-
	LD	-0.01	0.07	-0.08	-
	SP	0.21	0.26	-0.11	-
S.E.(s_{ij})[1]					
	LP	0.55			
	LD	0.07			
	SP	0.20			
S.E.(r_{ij})[2]					
	LP	0.92			
	LD	0.11			
	SP	0.20			

[a] LP = measurement in days, LD = measurement in mm, and SP = leafspot rating on a 1-5 scale.
[1] Standard error of the normal crosses
[2] Standard error of the reciprocal crosses

Table 3-19. Estimates of specific combining ability (SCA) effects on latent period (LP), lesion diameter (LD), and amount of sporulation (SP) measured on F_1 generation in the greenhouse study conducted at Chitedze Research Station, Malawi, during the 1990/91 growing season.

		Male Parent			
Female Parent	Component[a]	UF-P1	UF-P2	UF-P3	UF-P4
UF-P1	LP	-	1.87	-0.27	-0.01
	LD	-	-0.04	0.12	-0.08
	SP	-	-0.17	-0.11	-0.10
UF-P2	LP	3.34	-	2.00	-0.30
	LD	-0.34	-	-0.16	0.06
	SP	-0.48	-	-0.23	0.06
UF-P3	LP	1.00	-0.23	-	-0.56
	LD	0.00	0.07	-	0.10
	SP	0.17	0.02	-	-0.08
UF-P4	LP	-0.89	0.59	0.89	-
	LD	-0.13	0.03	0.15	-
	SP	-0.16	0.35	-0.24	-
S.E.(s_{ij})[1]					
	LP	1.78			
	LD	0.11			
	SP	0.15			
S.E.(r_{ij})[2]					
	LP	1.53			
	LD	0.16			
	SP	0.28			

[a] LP = measurement in days, LD = measurement in mm, and SP = leafspot rating on a 1-5 scale.
[1] Standard error of the normal crosses
[2] Standard error of the reciprocal crosses

three components of resistance were assessed. Mean squares for GCA and SCA were pooled over sites and GCA/SCA ratios computed on F_1, F_2, and F_3 generations for LP, LD, and SP. The ratios are presented in Table 3-20.

Although SCA appeared to be a significant source of variation in the studies (Tables 3-4, 3-10, and 3-16), it is evident (Table 3-20) that SCA accounted for a relatively small portion of the variation. For latent period, the variation accounted for by GCA mean squares was 4, 6, and 11 times greater than that accounted for by SCA mean squares in the F_1, F_2, and F_3 generations, respectively. Variation accounted for by GCA was also greater for lesion diameter and amount of sporulation (Table 3-20). This provides further evidence that the three components studied are controlled by additive gene effects. Holbrook (1990) reported variation in yield accounted for by GCA mean squares to be 10 and 15 times greater than that accounted for by SCA mean squares in the F_2 and F_3 generations, respectively.

Overall, the SCA effects, although significant, were small. This may have occurred because dominance and genetic interactions involving dominance (Griffing, 1956b) decrease rapidly with inbreeding; unless they are very large, they should be insignificant with increased levels of inbreeding.

Table 3-20. The relative magnitude of mean square (MS) for GCA and SCA for three components of resistance to late leafspot measured in F_1, F_2, and F_3 generations, pooled over sites.

	MS(GCA)/MS(SCA)		
Component	F_1	F_2	F_3
Latent period	3.8	5.7	10.8
Lesion diameter	1.9	2.0	9.0
Sporulation score	10.6	14.5	21.0

CHAPTER 4
COMPARISON OF COMPONENTS OF RESISTANCE TO LATE LEAFSPOT IN PEANUT GENOTYPES AND CROSSES MEASURED IN DIFFERENT ENVIRONMENTS

Introduction

The utilization of peanut (Arachis hypogaea L.) genotypes resistant to late leafspot (Cercosporidium personatum [(Berk. and Curt.) Deighton] in a peanut breeding program is important, but environmental conditions can be a major factor in the resistant reaction of a genotype. Variability in environment has been long recognized as an important factor influencing the performance of genotypes for a number of traits. This comes about due to changes in both biotic and abiotic factors which collectively bias the performance of the genotype. With change in the environment, the pathogen population may also change. Selection of genotypes for use in a peanut breeding program based upon the overall performance of the genotypes across locations is the best way to ensure stability.

Several workers (Anderson et al., 1986; Chiteka et al., 1988; Kornegay et al., 1980; Walls et al., 1985) have evaluated peanut genotypes for resistance to late leafspot in both greenhouse and field studies and have reported resistance in some genotypes in both environments. Other workers have

reported the opposite. Genotypes that performed well in the greenhouse did not do well in the field and vice versa and have attributed that to differences in pathogen population (Hassan and Beute, 1977; Cook, 1981), sample size (Jogloy, et al., 1987), evaluation techniques (Nevill, 1982), and genotype x environment interaction (Cook, 1981).

In some studies (Chiteka et al., 1988; Anderson et al., 1986) the researchers have looked at the relationships among components of resistance to late leafspot in greenhouse and field, to determine how the selection of one component would influence the other components. Chiteka et al. (1988) reported significant correlations among components of resistance measured on several peanut genotypes in both greenhouse and field and between components measured in the field and the greenhouse. Anderson et al. (1986) also reported significant correlations between components of resistance to late leafspot measured on F_1 and F_2 generations in field and greenhouse studies.

Studies comparing measurements of components of resistance to late leafspot from different countries were not found in the literature. The objectives of this study were 1) to assess stability of resistance to late leafspot by comparing measurements of components of resistance, latent period (LP), lesion diameter (LD), and amount of sporulation (SP) taken on parents and F_2 generation material evaluated in three environments; 2) to examine the relationships existing

among the three components of resistance between field and greenhouse studies; and 3) to determine whether late leafspot pathogen populations in the different locations were similar based on the measurements of the three components of resistance.

Materials and Methods

Four genotypes (Table 2-1) and twelve crosses (Table 2-3) originating from a 4 x 4 diallel cross were evaluated at Gainesville, Florida, USA, during the summer of 1990 and in Malawi, Africa, during the 1990/91 growing season. The genotypes and the crosses were evaluated for three components of resistance: latent period (LP), lesion diameter (LD), and amount of sporulation (SP).

In Florida, seed for the four genotypes and the twelve crosses were planted on 4 April 1990. The greenhouse study in Malawi was planted on 15 October 1990; the field studies were planted on 20 November 1990 and 27 December 1990. A randomized complete block design was utilized in all the studies.

In Florida, the seed were planted in single row plots, replicated two times. For the greenhouse study in Malawi, seed were planted in plastic pots and for the field studies, the seed were planted on two ridges, 90 cm apart. All studies were replicated three times. Data on the components of resistance from the field studies were collected on five plants; three plants were used for the greenhouse study. In

each study, three tetrafoliolate leaves were tagged from the selected plants. Other details about the studies, including inoculum production, inoculation of the target leaves, and data collection, were as outlined in Chapters 2 and 3.

Statistical Analysis

Data collected from the studies were subjected to statistical analyses. Analysis of variance (ANOVA) procedure (Littell et al., 1991) was done on each study for the three components; the General Linear Models (GLM) procedure was used for combined analysis of the data from all the locations. The GLM procedure was used because the number of replications and plants used in the studies were not uniform. A least significance difference (LSD) mean separation procedure (Steel and Torrie, 1980) was used to compare the means.

Sources of variation for the combined analysis were replicate, genotype, location, genotype x location, and error. Type III SS (Littell et al., 1991) from the GLM procedure were used to test for the significance of the sources of variation. The genotype x location interaction was used to test for the significance of replicate, genotype, and location (one field study at Gainesville, one greenhouse and two field studies in Malawi); the overall error was used to test for the significance of the genotype x location interaction.

To determine the relationship among the components of resistance within and between studies, correlation analyses (Steel and Torrie, 1980) were done. Pearson's correlation

procedure (SAS, 1988) was used.

Results and Discussion

Means for LP, LD, and SP for the F_2 generation are presented in Tables 4-1, 4-2, and 4-3. There were significant differences ($P<0.05$) among the genotypes and the crosses for all the components at all locations (Table 4-1, 4-2, and 4-3,). Genotype UF-P3 was the best for all the components at each of the locations followed by genotype UF-P1 and UF-P2; genotype UF-P4 was the poorest. Crosses involving genotypes UF-P1, UF-P2, and UF-P3, as female parents produced the best progeny for the three components of resistance measured (Tables 4-1, 4-2, and 4-3).

Significant differences ($P<0.05$) in reciprocal crosses were noticed in some crosses for each component, particularly those crosses involving genotypes UF-P1 and UF-P3. Genotype UF-P4 produced resistant progeny only when it was used as a female parent in combination with UF-P3. Even though UF-P4 is susceptible to CP, when combined with UF-P3, the resistant genotype, a high level of resistance is obtained in the F_2 and subsequent generations. These differences suggest that some cytoplasmic factor and additive genetic effects may control inheritance of the components. Other workers (Coffelt and Porter, 1986; Sharief et al., 1978) reported similar results.

Throughout the studies, crosses UF-P1 x UF-P3, UF-P2 x UF-P3, and UF-P3 x UF-P1 produced progeny with increased LP, reduced LD, and decreased SP. The ranking of the genotypes

Table 4-1. Mean LP for four parents and twelve crosses taken on F_2 generation in the field and greenhouse studies conducted at Gainesville, Florida, during the summer of 1990 and in Malawi, during the 1990/91 growing season.

Parent/ Cross	Florida	Malawi (field)	Malawi (g/house)	Overall means
		days		
UF-P1	28.0	26.5	27.3	27.3
UF-P2	27.1	26.0	28.0	27.0
UF-P3	31.7	31.1	31.3	31.4
UF-P4	25.0	23.9	25.0	24.6
UF-P1 x UF-P2	29.0	26.7	28.0	27.9
UF-P1 x UF-P3	29.0	27.4	29.8	28.7
UF-P1 x UF-P4	25.3	25.1	25.1	25.2
UF-P2 x UF-P3	31.9	29.0	30.4	30.4
UF-P2 x UF-P4	24.7	26.9	26.0	25.9
UF-P3 x UF-P4	21.7	26.4	29.1	25.7
UF-P2 x UF-P1	32.3	26.0	27.6	28.6
UF-P3 x UF-P1	28.8	26.6	26.9	27.4
UF-P3 x UF-P2	28.1	27.9	30.9	29.0
UF-P4 x UF-P1	29.4	26.6	26.0	27.3
UF-P4 x UF-P2	27.0	25.6	27.6	26.7
UF-P4 x UF-P3	29.9	26.7	28.7	28.4
Overall means	28.1	26.8	28.0	27.6
LSD (0.05)	2.9	1.2	1.4	1.8

Table 4-2. Mean LD for four parents and twelve crosses taken on F_2 generation in the field and greenhouse studies conducted at Gainesville, Florida, during the summer of 1990 and in Malawi, during the 1990/91 growing season.

Parent/ Cross	Florida	Malawi (field)	Malawi (g/house)	Overall means
	mm			
UF-P1	2.2	1.5	1.6	1.8
UF-P2	2.3	1.8	1.6	1.9
UF-P3	1.3	1.2	1.2	1.2
UF-P4	2.3	2.3	1.7	2.1
UF-P1 x UF-P2	2.3	1.3	1.7	1.8
UF-P1 x UF-P3	1.3	1.5	1.0	1.3
UF-P1 x UF-P4	2.2	2.1	1.8	2.0
UF-P2 x UF-P3	1.8	1.3	1.4	1.5
UF-P2 x UF-P4	2.3	2.7	1.8	2.3
UF-P3 x UF-P4	2.3	1.6	1.4	1.8
UF-P2 x UF-P1	1.8	1.5	1.7	1.7
UF-P3 x UF-P1	2.1	1.4	1.3	1.6
UF-P3 x UF-P2	2.1	1.4	1.5	1.7
UF-P4 x UF-P1	2.4	2.0	1.8	2.1
UF-P4 x UF-P2	2.3	2.1	1.6	2.0
UF-P4 x UF-P3	1.7	1.6	1.6	1.6
Overall means	2.1	2.1	1.6	1.8
LSD (0.05)	0.3	0.3	0.3	0.3

Table 4-3. Mean SP for four parents and twelve crosses taken on F_2 generation in the field and greenhouse studies conducted at Gainesville, Florida, during the summer of 1990 and in Malawi, during the 1990/91 growing season.

Parent/ Cross	Florida	Malawi (field)	Malawi (g/house)	Overall means
		1-5 scale		
UF-P1	2.3	1.7	1.9	1.9
UF-P2	2.3	2.2	2.1	2.2
UF-P3	1.8	1.7	1.1	1.5
UF-P4	2.3	2.9	3.0	2.7
UF-P1 x UF-P2	2.3	2.0	1.9	2.1
UF-P1 x UF-P3	2.0	1.8	1.5	1.8
UF-P1 x UF-P4	2.4	1.9	3.1	2.5
UF-P2 x UF-P3	2.2	1.9	1.6	1.9
UF-P2 x UF-P4	2.7	2.3	3.4	2.8
UF-P3 x UF-P4	2.2	2.1	1.7	2.0
UF-P2 x UF-P1	2.0	1.8	2.4	2.1
UF-P3 x UF-P1	2.2	1.9	1.3	1.8
UF-P3 x UF-P2	2.5	1.8	2.1	2.1
UF-P4 x UF-P1	2.6	2.4	2.7	2.6
UF-P4 x UF-P2	2.6	2.1	2.9	2.5
UF-P4 x UF-P3	2.1	2.1	1.9	2.0
Overall means	2.3	2.0	2.2	2.2
LSD (0.05)	0.4	0.2	0.4	0.3

and crosses varied slightly from location to location, but those genotypes and crosses that performed well at one location also did well at the other locations. Overall, the performance of the genotypes and the crosses was consistent across locations. It is evident from the non-significant ($P>0.05$) genotype x location interaction in Table 4-4 that the performance of the genotypes and the crosses was similar across locations.

These results further suggest that the pathogen populations were similar. Hence, genotypes selected in Florida would serve as a useful source of germplasm for a late leafspot resistance breeding program in Malawi.

Means for the components from the combined analysis of all the studies are presented in Table 4-5. Overall, genotype UF-P3 was the best for all the components, followed by UF-P1 and UF-P2. Genotype UF-P4 was the poorest for all the components. Additionally, progeny resulting from crosses between the three genotypes, UF-P1, UF-P2, and UF-P3 were resistant to late leafspot (Table 4-5). This is also consistent with results from diallel analysis (Chapter 3).

Correlation coefficients relating the components of resistance measured in field and greenhouse studies in Florida and in Malawi are presented in Table 4-6. All the components significantly correlated with each other. In Florida, LP negatively correlated ($P<0.001$) with LD ($r=-0.567$) and SP ($r=-0.671$); LD positively correlated with SP ($r=0.495$). From

Table 4-4. Mean squares for LP, LD, and SP from a combined analysis of field and greenhouse studies on comparison of components of resistance to late leafspot in peanut genotypes and crosses conducted at Gainesville, Florida, during the summer of 1990 and in Malawi, during the 1990/91 growing season.

Source of variation	df	Mean squares
	LP (days)	
Replicate	2	140.11
Location	3	510.36*
Genotype	15	429.67**
Genotype x Location	45	76.92
Error	65	187.69
	LD (mm)	
Replicate	2	0.42
Location	3	35.82**
Genotype	15	2.54**
Genotype x Location	45	0.77
Error	65	2.85
	SP (1-5 scale)	
Replicate	2	0.17
Location	3	52.25*
Genotype	15	29.01**
Genotype x Location	45	3.29
Error	65	12.09

*, ** Denote significance at the 0.05 and 0.01 probability levels, respectively.

Table 4-5. Overall means for LP, LD, and SP from a combined analysis of data from four locations on the study on comparison of components of resistance to late leafspot in peanut genotypes and crosses conducted at Gainesville, Florida, and in Malawi.

Parent/ Cross	Latent period (days)	Lesion diameter (mm)	Sporulation score (1-5 scale)
UF-P1	27.0	1.8	1.7
UF-P2	26.2	2.1	2.0
UF-P3	32.6	1.6	1.3
UF-P4	25.0	2.2	2.8
UF-P1 x UF-P2	26.6	1.9	1.7
UF-P1 x UF-P3	27.4	2.0	1.6
UF-P1 x UF-P4	25.5	1.9	2.4
UF-P2 x UF-P3	28.3	2.0	1.7
UF-P2 x UF-P4	27.8	1.8	1.8
UF-P3 x UF-P4	25.4	2.1	2.8
UF-P2 x UF-P1	27.8	1.8	1.5
UF-P3 x UF-P1	27.6	1.8	1.8
UF-P3 x UF-P2	27.8	1.9	1.5
UF-P4 x UF-P1	27.3	2.1	2.5
UF-P4 x UF-P2	26.7	2.0	2.0
UF-P4 x UF-P3	26.0	2.3	2.4
Means	27.2	1.9	2.0
LSD (0.05)	1.1	0.1	0.7

Table 4-6. Correlation coefficients relating three components of resistance to late leafspot in field and greenhouse studies conducted at Gainesville, Florida, in the summer of 1990 and in Malawi, during the 1990/91 growing season.

Component	Latent period (days)	Lesion diameter (mm)	Sporulation score (1-5 scale)
	Florida field study (1990)		
Latent period	1.000	-0.567***	-0.671***
Lesion diameter		1.000	0.495***
Sporulation score			1.000
	Malawi field study (1990/91)		
Latent period	1.000	-0.497**	-0.580***
Lesion diameter		1.000	0.389**
Sporulation score			1.000
	Malawi greenhouse study (1990/91)		
Latent period	1.000	-0.596***	-0.650***
Lesion diameter		1.000	0.439**
Sporulation score			1.000

, * Denote significance at the 0.01 and 0.001 probability levels, respectively.

the field studies in Malawi, LP negatively correlated with LD ($r=-0.497$) and SP ($r=-0.580$); LD positively correlated with SP ($r=0.389$). The trend of the relationships among the components for the greenhouse study was similar to those from the field studies (Table 4-6). LP negatively correlated with LD ($r=-0.596$) and SP ($r=-0.650$); LD correlated positively ($P<0.01$) with SP ($r=0.439$).

In general, genotypes and progeny with long LP had smaller lesions on the target leaves than those with short LP. Also, those genotypes and progeny with small lesions on the target leaves had reduced sporulation (Table 4-6).

It is apparent that while selecting peanut genotypes and progeny with long LP, we would simultaneously be selecting material with small LD and reduced amount of sporulation. This conclusion is consistent with general and specific combining ability results reported earlier (Chapter 3). Genotypes with large positive GCA effects for LP had large negative GCA effects for LD and SP; consequently crosses from these genotypes produced progeny with significant SCA effects for the three components of resistance.

Correlations between the components of resistance found in this study are in agreement with results obtained by others (Anderson et al., 1986; Nevill, 1982; Wynne and Walls, 1985). Also, Parlevliet (1979) noted moderate association between components of resistance in studies with rust in cereals, and observed that genotypes with long LP had lower SP.

Correlation coefficients relating measurements of the three components taken on the F_2 generations between greenhouse and field studies in Malawi and Florida, are presented in Table 4-7. Measurements of LP, LD, and SP were positively correlated with each other. LP moderately correlated with LD and SP. However, the correlation between LP and LD between greenhouse measurements in Malawi and field measurements in Florida was not significant. Overall, LP and SP measurements were the most consistent across locations.

Correlations between field and greenhouse studies in Malawi and between field studies in Florida and the greenhouse study in Malawi suggest that the components were very reliable for rating the genotypes for resistance across environments. Thus, the best genotypes and progeny in this study were equally stable against the late leafspot pathogen populations in Florida and in Malawi.

The results of this study support previous observations from other studies that peanut breeding lines that have increased latent period, decreased lesion size, and reduced amount of sporulation can be selected. Therefore, utilization of late leafspot resistant germplasm from the Florida breeding program would be beneficial for developing leafspot resistant cultivars in Malawi.

Table 4-7. Correlation coefficients relating measurements of three components of resistance to late leafspot taken on F_2 progenies in field and greenhouse studies conducted in Florida, during the summer of 1990 and in Malawi, during the 1990/91 growing season.

Component	Field Measurements (Malawi)		
	Latent period (days)	Lesion diameter (mm)	Sporulation score (1-5 scale)
Field measurements (Florida)			
Latent period	0.515*	-0.351*	-0.496*
Lesion diameter	-0.624**	0.636**	0.567*
Sporulation score	-0.582**	0.443*	0.635**
	Greenhouse measurements (Malawi)		
Field measurements (Florida)			
Latent period	0.528*	-0.406 NS	-0.474*
Lesion diameter	-0.477*	0.417*	0.437*
Sporulation score	-0.671***	0.539*	0.634**

*, **, *** Denote significance at the 0.05, 0.01, and 0.001 probability levels, respectively.

CHAPTER 5
CONCLUSIONS

The research discussed herein dealt with the inheritance of three components of resistance to late leafspot in peanut. Resistance to CP was evaluated in two locations, Florida and Malawi, to determine its stability across environments. To accomplish these objectives, genetic analyses were carried out on the data collected from all the locations. These included, generation means analysis, diallel analysis, regression analysis, and correlation analysis.

Performance of the F_1, F_2, and backcross generations was comparable to the best parental line for all the components in the Gainesville study. Further analysis of the data demonstrated that additivity was the predominant genetic effect occurring in more than half of the crosses. Dominance and epistatic effects were significant less frequent than additivity, implying that most segregating genes for the components exhibited little or no epistasis. The magnitude of the additive effects was small for all the components, indicating that environmental variance may have influenced measurements of the components. The predominance of the additivity in the components should make incorporation of resistance genes into agronomically useful peanut lines feasible. This is because genes for the susceptible or

resistant disease reaction would not be masked by other dominant or epistatic alleles.

These studies demonstrated that LP, LD, and SP are highly heritable components of resistance and that they are quantitatively inherited. Also, additive gene effects are of major importance in controlling these components. Thus, selection for improved resistance based on latent period, lesion diameter, and amount of sporulation should be possible in early segregating populations. However, the selection would depend on the sensitivity of the host-pathogen interaction as influenced by changes in environmental conditions. Because of the host-pathogen interaction with the environment, selection of genotypes based on replicated progeny performance would most likely provide maximum genetic progress.

Heritability estimates, based on parent-offspring regression were moderate to high. Narrow-sense heritability estimates across locations were 0.60 for LP, 0.52 for LD, and 0.41 for SP. Realized heritability estimates were 0.69 for LP, 0.63 for LD, and 0.52 for SP. Amount of sporulation was affected more by environmental variation than latent period and lesion diameter.

General combining ability was significantly higher than specific combining ability and reciprocal effects for all the components. However, reciprocal cross differences were manifested in some crosses implying that a cytoplasmic factor

and additive genetic effects may control leafspot resistance.

In all studies, and across locations, the three components significantly correlated with each other. LP negatively correlated with LD (r=-0.55) and SP (r=-0.63); LD positively correlated with SP (r=0.44). Positive correlations were also noticed among the components between the Florida and the Malawi studies. This implies that the components were stable against the late leafspot pathogen populations across environments. This may also mean that the pathogen populations in Florida were similar to that in Malawi. Consequently, utilization of the Florida germplasm would be beneficial in developing late leafspot resistant cultivars in Malawi.

APPENDIX A
GLOSSARY OF TERMS

Additive gene effects: gene action in which the effects of a genetic trait are enhanced by each additional gene, either an allele at the same locus, or genes at different loci. Additive genes contribute to the additive genetic variance.

Dominant gene effects: gene action with deviations from the additive such that the heterozygote is more like one parent than the other.

Epistatic effects: interaction between nonallelic genes in which a gene exerts a dominant effect over a gene at another locus.

General combining ability (GCA): the average or overall performance of a genetic strain in a series of crosses.

Heritability: a portion of observed variance in a progeny that is inherited. This is what determines the degree of resemblance between relatives.

Narrow-sense heritability: heritability estimated from the additive portion of the genetic variance.

Realized heritability: response per generation that is related to the selection differential. Thus, $H_R = R/S$; where, R = response and S = selection differential.

Specific combining ability: the performance of specific combinations of genetic strains in crosses in relation to the average performance of all combinations.

APPENDIX B
MAXIMUM AND MINIMUM TEMPERATURE FOR GAINESVILLE, FLORIDA, FOR THE PERIOD APR-AUG 1989 AND 1990

	1989 Temperature °C		1990 Temperature °C	
Week ending	Maximum	Minimum	Maximum	Minimum
1-Apr	28.0	13.4	28.2	12.5
8-Apr	26.5	7.6	24.9	10.4
15-Apr	23.3	10.0	24.7	8.6
22-Apr	28.8	13.8	28.7	11.0
29-Apr	30.2	11.1	28.8	13.6
6-May	30.2	14.9	32.5	17.3
13-May	28.7	10.1	27.9	13.7
20-May	31.0	13.9	32.5	18.3
27-May	31.5	17.3	31.7	17.8
3-Jun	35.2	19.5	32.3	17.9
10-Jun	32.6	19.4	32.9	19.3
17-Jun	34.2	20.4	32.6	17.9
24-Jun	32.6	19.3	34.4	20.7
1-Jul	32.9	20.2	32.1	18.9
8-Jul	32.2	20.7	32.9	21.0
15-Jul	34.9	20.5	34.3	20.1
22-Jul	32.1	21.7	31.3	20.5
29-Jul	32.9	20.6	33.8	20.4
5-Aug	34.6	20.6	34.3	19.9
12-Aug	33.2	21.1	33.4	19.8
19-Aug	31.3	19.3	32.9	19.9
26-Aug	34.4	21.4	32.3	20.4

APPENDIX C
MAXIMUM AND MINIMUM TEMPERATURE FOR KASINTHULA EXPERIMENTAL STATION, MALAWI, FOR THE PERIOD NOV 1990-MAR 1991

	Temperature °C	
Week ending	Maximum	Minimum
7-Nov	37.0	20.6
14-Nov	35.9	21.1
21-Nov	38.1	24.9
28-Nov	33.6	23.0
5-Dec	36.6	23.7
12-Dec	36.4	23.4
19-Dec	39.4	24.1
26-Dec	36.4	24.1
2-Jan	34.0	22.7
9-Jan	33.4	23.3
16-Jan	30.6	23.0
23-Jan	35.3	24.1
30-Jan	34.7	24.0
6-Feb	35.0	24.0
13-Feb	32.6	24.0
20-Feb	32.4	23.6
27-Feb	35.5	23.7
6-Mar	35.7	24.1
13-Mar	32.3	23.0
20-Mar	33.9	23.4
27-Mar	31.4	23.4

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BIOGRAPHICAL SKETCH

Allan James Chiyembekeza was born on 5 June 1954, in Thyolo district, southern region of Malawi. He attended Molere Full Primary School, Thyolo and Mtendere Secondary School, in Dedza district, central region.

In 1974, he enrolled for a B.Sc. degree with the University of Malawi, Chancellor College. After one academic year at Chancellor College, he transferred to Bunda College of Agriculture (a constituent college of the University of Malawi) from where he graduated with a B.Sc. degree in agriculture. Upon graduation, he was employed as a groundnut breeder by the Malawi Department of Agricultural Research.

In 1983, he was awarded a USAID scholarship under the USAID/UF/Malawi contract, to study for an M.S. degree in agronomy at the University of Florida, beginning in the spring of 1984. After completing his studies in October 1985, he returned to Malawi and resumed his duties as a groundnut breeder. In 1986, he was awarded a three months' in-service fellowship by ICRISAT, to interact with the scientists in the Legumes Improvement Program, at ICRISAT center in India.

Under the sponsorship of the Malawi government, he returned to the University of Florida in the fall of 1988 to pursue a Ph.D. degree in agronomy, specializing in peanut

breeding (genetics of late leafspot resistance). In 1990, he received a research grant from the Rockefeller Foundation under the African Dissertation Internship Award Program, which enabled him to do part of his Ph.D. dissertation research in his home country, Malawi.

Allan is married to Eleanor, the last but one daughter of Mr. and Mrs. G. Magwira. He has seven children.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

David A. Knauft, Chairman
Professor of Agronomy

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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

May, 1992

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